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# Preface

May 20th 2012 was the tenth anniversary of Stephen Jay Gould's death. Palaeontologist at the Museum of Comparative Zoology, Harvard University, eminent evolutionary biologist, science writer, science historian and opinion maker, Gould gave us an extended and revised version of the theory of evolution, his "Darwinian pluralism", which is still today an interesting frame to understand the scientific advancements in many evolutionary fields. His anticipating insights about the conjunction of evolution and development, the role of ecological and biogeographical factors in "punctuated" speciation, the need for a multi-level interpretation of the units of selection, the interplay between functional pressures and internal constraints in processes like exaptations and spandrels are fruitful current lines of experimental research today.

Even his pungent and sometimes very radical controversies against the progressive representations of evolution (especially human evolution), biological determinism, pan-selectionist and a gene-centered view of natural history, or the adaptationist "just-so-stories", have left their mark in contemporary biology. Gould's "histories of nature" were explorations in the "nature of history," with wider cultural and philosophical implications, like his crucial concept of contingency. Thus, after 10 years of new discoveries and unforeseen advances, it is worthy to discuss the efficacy and limits of Gould's pluralism as renovation of the Darwinian research program.

At the historical location of the Istituto Veneto di Scienze, Lettere ed Arti in Venice, the town of Gould's "spandrels of San Marco", an international panel of scientists and philosophers—including Gould's closest friends and colleagues like Niles Eldredge, Elisabeth Lloyd, and (in video) Richard Lewontin—discussed his evolutionary and anthropological legacy, his idea of science as a complex rational enterprise, evolving itself and immersed in human society, his proposal for a methodology in historical sciences, and his unmistakable style of writing and argumentation, overcoming the boundaries between science, literature, and art. In Gould's production, scientific research and communication of science were two fields of inquiry strictly related by the idea that science is a high expression of human curiosity and culture.

The International Meeting was held at the Istituto Veneto, with the collaboration of University Ca' Foscari, on May 10–12th 2012. We thank Maria Turchetto and Elena Gagliasso for their helpful participation in the organizing committee. The Venetian meeting has been the basis for the construction of this volume, which is divided into four parts. The first one—with the contributions of Niles Eldredge, Elisabeth Lloyd, and Telmo Pievani—is focused on the general scientific legacy of Stephen J. Gould as an evolutionary biologist: the unpublished history of the birth of Punctuated Equilibria; the role of Gould's criticism against adaptationism; the structure of his "Darwinian pluralism". The second part—with the contributions of T. Ryan Gregory, Alessandro Minelli, Gerd Müller, and Marcello Buiatti—is dedicated to the discussion of Gould's theoretical innovations seen from the perspective of genomics and developmental biology: the Gouldian idea of genome as a hierarchical system; the debate about the levels of selection and the "individual" units in evolution; his anticipations of some fundamental "Evo-Devo" concepts like developmental constraints and spandrels; his intuitions about the complexity of genetic coding and differential mutation rates. The third part—with the contributions of Ian Tattersall, Guido Barbujani, Klaus R. Scherer, and Winfried Menninghaus—deals with the important anthropological legacy of Stephen J. Gould: his advocacy of a highly branching phylogeny of hominids, against any progressive idea of cumulative change in human evolution; his bold fight against biological determinism and the alleged genetic foundations of the concept of "human races," the evolution of emotions, speech, and music in a Gouldian perspective. The fourth part—with the contributions of Andrea Cavazzini and Alberto Gualandi—is focused on some aspects of Gould's legacy in human sciences, with reference to the conceptual shifts between economics and evolutionary theory, and the possibilities and limits of Gould's humanism.

The richness of Gould's production and intellectual inheritance cannot be covered by a single collections of essays. Nevertheless, we hope to add another piece to the rich mosaic of studies that the Harvard evolutionist deserves. Gould's "industry" is a mine of historical hints, epistemological proposals, scientific insights, and contentious theories. As Richard Lewontin said in his thoughtful opening address by video conference, Gould's way of exploring evolution was a mix of pure history and theoretical generalizations, aided by extraordinary communicational skills and a worldwide reputation. He was so brilliant inventing metaphors (such as "spandrels" and "Punctuated Equilibria"), that he was able to depict for professionals, and for the general audience at the same time, the wide frame of the "multiple generating forces of evolution."

He was a forerunner. He challenged several orthodoxies, included the "ultra-Darwinian" one. He became a straw-man for many opponents. Still now, he is one of the most quoted evolutionists. During these first ten years his proposals and provocations have had a differential survival, but there are no doubts that his pluralism has strongly influenced the current debate. Stephen J. Gould is a present-day evolutionist.

Gian Antonio Danieli
Alessandro Minelli
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# Part I
# Evolutionary Theory

# Stephen J. Gould in the 1960s and 1970s, and the Origin of “Punctuated Equilibria”

**Niles Eldredge**

**Abstract** Steve Gould arrived as a beginning graduate student in the Department of Geology at Columbia University in the Fall of 1963. He was one of a group of entering students interested in paleontology, biostratigraphy, paleoecology and, of course, evolution. Though I was still an undergraduate, I was welcomed into the group—and took part in the field trips and special seminars they organized: especially one on paleontology and evolution whose main inspiration was Steve himself. Most of these students eventually went on to have distinguished careers in paleontology and related fields.

Steve’s initial—and perhaps always his favorite—professional passion was morphology, development and evolution. He astonished everyone that he would devote an entire year away from his doctoral research to write an exploratory review paper on allometry—inspired by his initial work as an undergraduate with John White on the meaning of “b” in the famous equation $Y = bX^k$. Steve quickly emerged as a model of the ambitious young professional, encouraging us all to develop and publish research projects—and to be bold and think about theoretical issues. He once said to me Why wait until we are 60 before we publish on evolutionary theory? And of course he was right; indeed, sadly, he did not live beyond that very age.

The genesis of our 1972 paper *Punctuated Equilibria*: *An Alternative to Phyletic Gradualism* has been recounted several times, by Steve and by myself as well as by others. The definitive version, in my view, is in the newly published book *Rereading the Fossil Record* (2012) by historian David Sepkoski. I will review the essential details of our joint participation in Tom Schopf’s GSA Symposium and multi-authored book, both entitled *Models in Paleobiology*. Though the gist of the concept of punctuated equilibria was developed in my 1971 paper *The Allopatric*

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*Model and Phylogeny in Paleozoic Invertebrates*, both Steve and I added material developing and extending the concept beyond its bare essentials.

What were those essentials? Simply, the juxtaposition of the concept of allopatric speciation and the empirical demonstration of stasis—the fact that most species show little if any lasting morphological change throughout their often quite long histories. Change for the most part comes at speciation, and quiescence is the norm from then on.

I will also add a codicil that I believe would have intrigued Steve very much: Darwin, as a young man in his late 20s, saw that the birth of species in isolation (the "allopatric speciation" of Dobzhansky and Mayr, so essential to our own notion of "Punctuated Equilibria") would account for the persistence of species, unchanged, "through thick formations"—in other words, our concept of "stasis." Darwin contrasted this vision with the inevitable gradual change of species—a vision of evolution he came to favor and promote, though he lacked empirical evidence for it.

With the birth of species in isolation, Darwin reckoned that adaptive change through natural selection happens rapidly in small populations. But with the passage of geological time and the inevitable environmental change that occurs, Darwin thought that natural selection would be constantly modifying entire species slowly and gradually. He could not reconcile the two views—and so his problem was deciding which was the most likely context for adaptation via natural selection to occur. He chose what we later called "phyletic gradualism."

That young Darwin would have liked our title, but would probably have insisted on one minor change: *Punctuated Equilibria: The Alternative to Phyletic Gradualism.*

I think Steve would have enjoyed knowing that.

## 1 Introduction

When Stephen Jay Gould died on May 20, 2002, he was arguably the most famous scientist in America, and perhaps in the entire world—ranking right up there with predecessors like Margaret Mead and Carl Sagan. Much of this fame was, of course, engendered by his so-called "popular" writing—but Steve told me long ago that successful writing styles do not change to embrace wider audiences: only the vocabulary changes. Steve felt that all of his writings, from the more narrowly technical to the most broadly engaging, were of the same intrinsic merit, reflecting fundamentally his same intellectual values. Steve owed his success, in large measure, to his skill in making his readers feel they are directly involved in his intellectual adventures.

But it was as fledgling paleontologists and evolutionary theorists that Steve and I first met, forging a lasting bond that, in less than a decade, produced what was probably Steve's—and my own—arguably most important and certainly well-known piece of scientific work: the theory of "Punctuated Equilibria." My goal here is to explore aspects of the educational experiences we shared, along with fellow students, in the Geology (and, to a lesser degree) Zoology Departments at Columbia University in the mid-1960s; to reflect on Steve's talents and proclivities as a young, career-minded scientist in those years; and to characterize the circumstances and, especially, the underlying evolutionary issues and empirical data that led to the publication of "punctuated equilibria" in the early 1970s. I will conclude with a brief analysis of the deep, if forgotten, intellectual roots of Punctuated Equilibria—concluding that both allopatric speciation and what we called punctuated equilibria, both clearly conceived by Darwin but never published, simply had to be rediscovered and elaborated on in the 20th century.

## 2 Steve Gould's Impact on Fellow Fledgling Paleontologists at Columbia in the 1960s

Steve Gould showed up on the Columbia campus in the Fall of 1963, newly-graduated from Antioch College, and now-enrolled in the invertebrate paleontology program at Columbia's Department of Geology. He was joined, significantly, I think, by at least a half-dozen other aspiring paleontologists or stratigraphers—among whom was H. B. Rollins. Most of these new students went on to have productive and distinguished careers. I think the sheer size of this entry class was critical to the dynamics of the learning process—as they did, as students often do, take their intellectual life largely into their own hands.

In the Fall of 1963, I was a junior in college, and having decided that I would stay in the academic world, I was trying to make up my mind whether I would go into physical anthropology or geology/paleontology. I was smitten by this intellectually active new group of graduate students—and was delighted that they let me hang around. John Imbrie was then the invertebrate paleontologist on the Columbia campus (with Norman D. Newell and Roger L. Batten, at the American Museum of Natural History, acting as adjuncts within the Columbia Geology Department). I was taking Imbrie's introductory paleontology, followed the next semester by biostratigraphy, which was open to graduate students.

But the really important thing was that, probably with Steve as ringleader, the new graduate students saw that there was little in the way of evolution in the curriculum. So, they started their own seminar, and they let me join in. We read extensively, and, taking turns, each of us led discussions. At one point I did a session on macroevolution. This was when Steve's influence on all of us quickly emerged. He believed that no one should wait until they are sixty (ironically, his age when he died) before they start actively thinking, talking and writing about theoretical issues. And, for that matter, publishing on them!

Paleontology, then as now, was usually split between invertebrate and vertebrate programs—and at Columbia, at least, vertebrate paleontology, ever since the days of Henry Fairfield Osborn in the last decade of the nineteenth century, lay in the province of the Zoology (now Biology) Department. Vertebrate Paleontology was seen as the more intrinsically biological subject—with its focus on the anatomy of fossil bones, and their relevance to deciphering phylogenetic relationships. That was the supposed route to take if one wanted to contemplate evolutionary issues from the standpoint of the fossil record.

In contrast, invertebrate paleontology was usually pursued in geology departments; certainly this was always the case at Columbia. Though some invertebrate paleontologists—including Norman D. Newell, who was mentor to both Steve and myself—had active interests in ecology and evolution, traditionally invertebrate paleontology had been studied largely as a means of correlating rocks, thus producing a repeatedly tested framework of geological time. And though much of the interest in this aspect of invertebrate paleontological research lay in its economic implications for the search for oil and gas reservoirs, the discipline of biostratigraphy (the spatio-temporal distribution of species in the fossil record), especially as developed in the nineteenth century in Europe going all the way back as far as Cuvier, had clear implications for understanding patterns—thus potentially processes—of evolution.

Why did Steve Gould, so famous for having fallen in love with the American Museum's *Tyrannosaurus* at age 5, decide to pursue invertebrate paleontology rather than the more traditionally biologically and evolutionarily-minded vertebrate paleontology? I think the main reason was simply Steve's undergraduate experience with the invertebrate paleontologist J. F. White at Antioch. Steve's very first paper (published as White and Gould 1965) was on the meaning of "b" in the famous equation $Y = bX^k$, used variously to describe allometric growth of individuals, series of individuals within populations—or even evolutionary changes between closely related species in a lineage. Steve had discovered (or Prof. White had shown him) an unwrapped, unstudied collection of Bermudan Pleistocene land snails in the basement of the Geology Department at Antioch—and Steve had been smitten with the geometric growth of these well-preserved snails—and had vowed to one day make them the subject of his doctoral dissertation. Few people arrive at graduate school already knowing the precise topic of their future Ph. D. dissertation!

A glance at Steve's earliest entries on his prodigious bibliography reveal his passion for growth and form, and for morphology in general. We were all aghast when Steve took an entire year off from his doctoral research to answer the invitation from the journal *Biological Reviews* to write a review of the literature on allometry—an opportunity Steve used to make fresh observations on the subject, especially its relationship to evolution (Gould 1966). Steve saw that invitation as a golden opportunity—and, as was to be his hallmark, he jumped on the chance and worked extremely hard on it. I have always said that I never met anyone so smart who worked so hard as Steve Gould. He was establishing a reputation as an original thinker on theoretical issues—and laying the groundwork, both in substance and style, for his first book *Ontogeny and Phylogeny* (Gould 1977).

Thus Steve, at heart, was first and always a morphologist and developmentalist. One of his most important and original insights came towards the end of the

1970s—when he was among the first to point out that regulatory genes, depending upon their actions, and when in ontogeny they are switched on, can have a disproportionately large effect in modifying adult morphologies in the evolutionary process: long-since a central tenet of evolutionary developmental biology—or "evo-devo."

And, I must also say, in an evolutionary context, Steve was as much of an adaptationist as the next person. I know it sounds strange to say so, given his reputation as a critic of hyperadaptationism—and his search for alternative explanations for morphological change in evolution (as witness his enthusiasm for Elisabeth Vrba's concept of "exaptation"—published as Gould and Vrba 1982—though the initial idea had been developed by Vrba). All that is true—but at heart he was a neo-Darwinian always. As am I—and so are we all.

Once, after a seminar at the American Museum sometime after 1965 (when I had graduated from Columbia College and had taken my own place in the Columbia graduate program), he said in mock-serious despair "sometimes I think that man will renounce natural selection on his death-bed"—referring to our august mentor Norman D. Newell, who seemed to include everything but natural selection when discussing the history of life, and how it all came to be, with his students (Fig. 1).

Newell, we were slowly beginning to realize, was the only person in the mid-twentieth century who took patterns of what we now call "mass extinctions" seriously—and insisted that they deserve special study to elucidate their causes

**Fig. 1** Stephen Jay Gould (*left*) and Niles Eldredge (*right*) flanking their mentor, Norman D. Newell (*seated*) on the occasion of Dr. Newell's 90th birthday celebration at the American Museum of Natural History in New York in February, 1999. Photo by Gillian Newell

(e.g. Newell 1963). He also insisted that they periodically have an enormous impact (literally and figuratively) on the history of life, thus opening the door still further to seeing a causal interrelationship between evolution and its converse: extinction.

For a time, we callow graduate students openly wished Newell would discuss evolution—not extinction. Emphasize the positive, not the negative! And it was only later—indeed, not until the 1980s—when we were immersed in our professional pursuits at different institutions, that the Alvarez hypothesis on the end-Cretaceous mass extinction made such headlines, and it began to become clear that much, if not all, evolution occurs only after episodes of ecosystem disruption, sufficiently widespread and severe to cause the extinction of entire species—and in the most dramatic and easily seen cases—of higher taxa.

But how, exactly, to study evolution in the invertebrate fossil record? After all, with just the remains of their exoskeletons, it was often hard to discern the adaptive significance of much of the morphology of invertebrate fossils.

No one back in the 1960s knew that evolutionary theory literally had begun with the work of Jean-Baptiste Lamarck in France (Lamarck 1801; also 1809) and Giambattista Brocchi in Italy (Brocchi 1814; see also Dominici 2010 and Dominici and Eldredge 2010)—both of whom had brought a quantitative aspect to their consideration of Tertiary fossil mollusks. But, on the other hand, Norman Newell had already conducted several studies on evolutionary lineages in Upper Paleozoic bivalves in the 1930s and 1940s (e.g. Newell 1938, 1942)—and Tom Waller, an older graduate student working under Newell at the American Museum, was already deeply immersed in a detailed study of scallop evolution in the Tertiary Atlantic and Gulf coastal deposits of North America. Tom was using bivariate statistics as a cornerstone of his characterization and comparison of scallop morphologies in space and time.

And then there was the simple fact that it was the 1960s—and computers were just appearing on major university campuses. Columbia got its first IBM 7090/7094 computer system sometime around the mid-1960s, and many of us soon found ourselves scurrying over to the Computer Center clutching shoeboxes crammed with those old IBM punch cards. And we were lucky that John Imbrie, picking up on the newly found passion for multivariate statistical analysis then beginning to infiltrate geology in general, introduced all of us who were adventurous to the intricacies and potential analytic power of Factor Analysis, Multivariate Analysis of Variance, the Mahalanobis $D^2$ statistic—and other arcane statistical delights. Steve was already immersed in statistical analysis with his interests in allometry—and my second published paper (Eldredge 1968) was entitled *Convergence of Two Pennsylvanian Gastropod Species: A Multivariate Mathematical Approach*.

In short, circumstances themselves converged to cry out for studies of evolution in the fossil record. We quickly saw that, whatever the disadvantages that many invertebrate fossil taxa have for old-fashioned evolutionary studies purporting to document adaptive change through time, these were more than outweighed by the availability of statistically meaningful samples in well-chosen study groups.

And one more factor played a key role in these studies: Dobzhansky and Mayr, still dominant figures, had shown in the 1930s and 1940s (e.g. Dobzhansky 1935, 1937; Mayr 1940, 1942) the critical importance of geography and isolation in the evolutionary process. It would be as important to study patterns of geographic variation in more or less contemporaneous populations within a lineage—as it would be to chart the course of morphological change (and, as it quickly turned out, the non-change we later called "stasis") through time.

Steve stuck to his guns and did his Pleistocene Bermudan land-snails—calling it (in an early example of the apt, often perfect, metaphors he became famous for) a "microcosm." The snails were isolated there on this small island, preserved in sediments reflecting two contrasting sorts of environmental conditions. He had no idea that, in studying fossils of a lineage of which there were still-living, surviving species, he was actually working on what I have come to see as the Ur-question of evolutionary biology: the search for a natural causal explanation for the origin of the species comprising the modern biota.

In contrast, I went to the Paleozoic—a disadvantage, as the old-timers like Brocchi saw, because none of the species present as fossils in the Devonian had anything directly to do with the origin of our modern fauna. But I had complex anatomy (my fossils were trilobites), and large populations spanning nearly half the North American continent in breadth, as well as prodigious amounts of geological time (6–8 million years—now considered to have been closer to 6 than 8 million years).

In a nutshell, I found that my trilobites—my *Phacops rana*—showed such stability, such lack of change through time, that I despaired of finding any evolution at all. But I saw it happening laterally, and it was clear that the allopatric model—geographic speciation—was the only way to make sense of my patterns in terms of modern evolutionary theory. I wrote these conclusions up in my Ph. D. thesis (Eldredge 1969), and I took that material and revamped it for the journal *Evolution*, submitted in 1970 and published as *The Allopatric Model and Phylogeny in Paleozoic Invertebrates* (Eldredge 1971) (Fig. 2).

Meanwhile, Steve had finished his evolutionary analysis of different stocks of *Poecilozonites* (later published as Gould 1969)—and, in 1968, headed off to begin his impressive career at Harvard—where he joined that rarified group of evolutionary biologists that included Ernst Mayr, Dick Lewontin and E. O. Wilson, and overlapping just briefly with the great evolutionarily-minded paleontologist George Gaylord Simpson.

I, in contrast, happily stayed in New York, accepting an appointment as an Assistant Curator in the Fossil Invertebrates Department at the AMNH, and an Adjunct Assistant Professorship at Columbia, in 1969.

Thus our days of occupying nearby offices in Schermerhorn Hall at Columbia, attending seminars at the AMNH—and, perhaps most critically—riding back and forth between Columbia and the Museum several times a week on the #11 bus, were over. Those bus rides were amazing. Almost invariably, Steve would launch into a soliloquy, telling me a story about something or other he had recently read—something intriguing to him that he had picked up in the literature. These rides

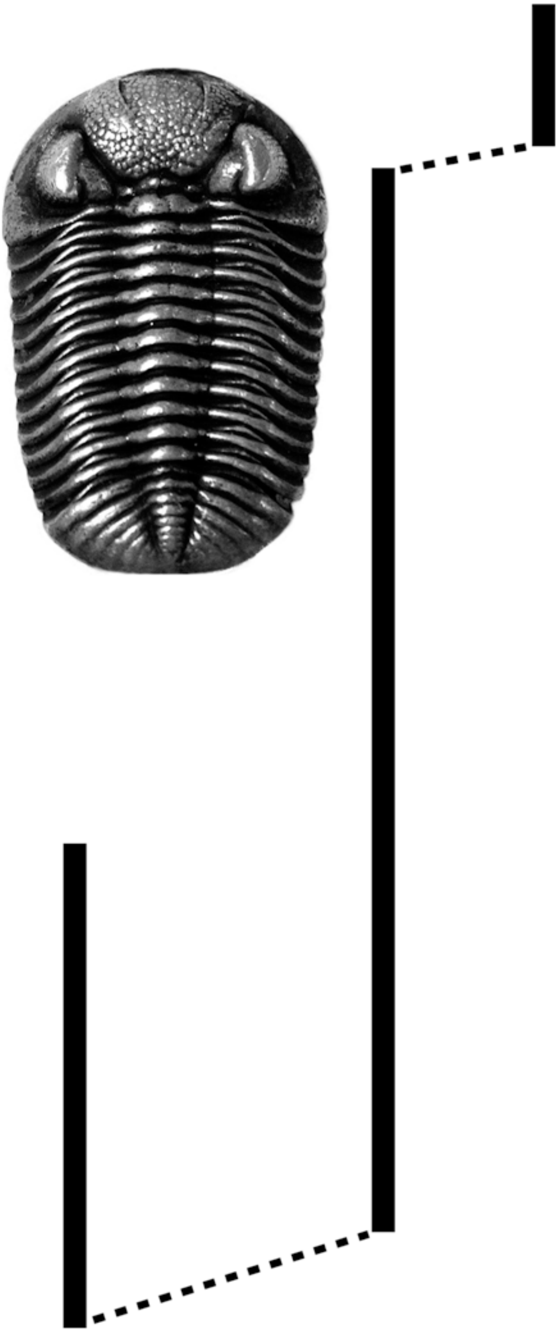

**Fig. 2** The evolution of the Devonian trilobite *Phacops rana* lineage—the original empirical example of “punctuated equilibria”

were invariably entertaining and sometimes astonishing. So I had no trouble at all, when the editor of *Natural History* magazine asked me if I could recommend someone to replace his outgoing columnist (my earlier mentor and role model, the anthropologist Marvin Harris); without giving it a second thought, I said "Steve Gould. He's never at a loss for words and always has a good story to tell"—or words to that effect.

But if the old student days together, with our wives and fellow students, were over, my working relationship with Steve in a very real sense was just getting going.

## 3 Punctuated Equilibria

Both Steve and I (e.g. Eldredge 2008), as well as others, have written on the history of the production of the actual paper we entitled *Punctuated Equilibria: An Alternative to Phyletic gradualism*—published as Eldredge and Gould 1972 in a multi-authored book entitled *Models in Paleobiology*, edited by invertebrate paleontologist Thomas J. M. Schopf. Fortunately, what I consider to be the definitive, canonical history of the circumstances and events—including a detailed analysis of the manuscript as it went through its pre-publication revisions, specifying in detail who wrote what when—has just been published by historian David Sepkoski (Sepkoski 2012) in his important new book *Rereading the Fossil Record. The Growth of Paleobiology as an Evolutionary Discipline.* Sepkoski reports that, as the son of the late Jack Sepkoski—a marvelous early developer of quantitative, "taxic" paleobiology, and one of Steve Gould's first graduate students—he was perhaps especially privy to the files and archives pertaining to the development of the entire discipline in the 1970s and 1980s, including the early contribution of "punctuated equilibria." I find his account lucid and accurate—and written with the dispassionate eye of an excellent historian. Indeed, it is somewhat prepossessing to find one's own actions, and those of his colleagues, from so long ago, described so truthfully—and, to me—as if it had happened just yesterday. Steve, I am sure, would have felt the same way had he survived to read David Sepkoski's book.

So the details are all out there and readily available, and I need not belabor them here—except to sketch briefly a few of the most basic points. For more information, readers should consult Sepkoski's book; as I am sure Steve would agree, in the immortal words of New York Yankes manager Casey Stengel, now "you could look it up"!

Steve, as I have said, had departed for Harvard—and was well on his way, working, if anything, harder than ever and participating as fully as possible in intellectual activities within—and even beyond—the strict confines of paleontology. Steve got wind of Tom Schopf's plans to organize a symposium for the 1971 Geological Society of America annual meeting, coupled with a book of the same title to be published afterwards. Hoping to join in, Steve unsurprisingly asked for the title "Models in Morphology," or perhaps "Models in Phylogeny." Schopf told him that Dave Raup had already accepted the morphology assignment, and

Michael Ghiselin the one on phylogeny. Steve had to take the next best thing, so far unassigned: "Models in Speciation."

Steve evidently thought about it—and then, getting in touch with me, said something to the effect that he couldn't think of much else to say beyond what I had written already and sent to him for comments—namely, the "Allopatric Model" manuscript that was published in 1971 in *Evolution*. He asked me to be coauthor and I said "sure"—and either then, or shortly thereafter, he proposed that he give the talk at the meeting and be senior author of the GSA meeting abstract, while I would write the initial draft of the full paper, and be senior author, of the published version of the paper. Sounded OK to me: I didn't especially like giving talks, as Steve unnecessarily reminded me—and in any case it always seemed far better to be senior author of a published paper than of an abstract of a talk at a symposium.

I was already thinking that the two papers held the potential of igniting a lot of interest and perhaps controversy—in paleontology, but also in evolutionary theory: primarily because one of the claims, based on empirical evidence and held out to be general, deviated far from the norm of conventional thinking. About which more below.

I wrote that first draft—including an account of Steve's thesis research on Bermudan snails, cast explicitly now into the context of the two main thematic components of our proposed theory. I also added an extra discussion, not previously agreed upon with Steve, on what I saw was a major implication of punctuated equilibria.

Steve came back with a greatly expanded essay, improving the rhetoric, making the argument more forceful, clarifying some concepts, and adding some thoughts on macroevolution of his own. And, crucially, he named not only the theory itself ("Punctuated Equilibria"), but also the phenomenon of species stability through long periods of geological time ("stasis"), as well as the vision of adaptive evolutionary history comprising inexorable gradual modification of entire species through time ("Phyletic Gradualism"). There is a lot to names, and our title, *Punctuated Equilibria: An Alternative to Phyletic Gradualism*, given what I just said about Steve's bestowal of names, was entirely Steve's.

I must say, however, that late in his life I asked Steve about why he had started calling our baby "punctuated equilibrium" instead of the original "punctuated equilibria." At first he affected not to understand what I was talking about, and basically denied having done so. Whatever the reason, I personally detest the term "punctuated equilibrium."

So what were the two thematic components of "punctuated equilibria?" (Fig. 3). Firstly, and contrary to popular and professional belief, and contrary especially to the enduring message of Charles Robert Darwin, we postulated that there is little if any empirical evidence that entire species will change slowly, gradually and progressively through geological time—such that new species in general evolve gradually from old. Phyletic gradualism is *not* a valid general model for the generation of morphological change, adaptive or not, in the evolutionary history of life. Rather, species, however variable locally and

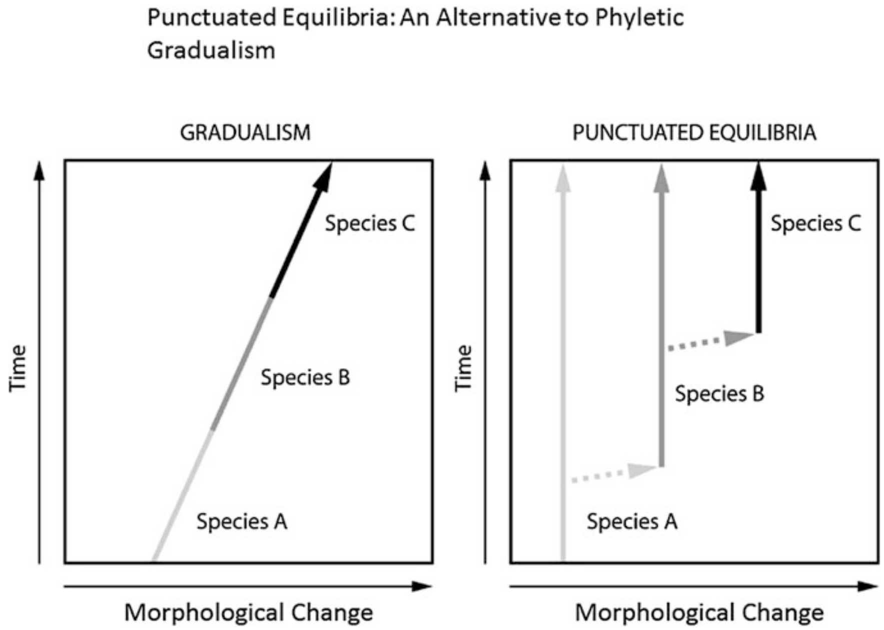

**Fig. 3** Comparison of "phyletic gradualism" and "punctuated equilibria" evolutionary patterns

geographically, typically do little more than oscillate (in terms of mean values of this or that morphological attribute) through what can be astonishingly long periods of time—in the case of marine invertebrates usually 5 million years or even longer. This is what we meant by the term "stasis."

As to the second component, it was simply the application of Dobzhansky and Mayr's notion of geographic ("allopatric") speciation: the origin of new species, with at least a modicum of adaptive change, usually if not invariably detectable on the morphological level, to explain the appearance of species from "offstage"—from elsewhere; and the common, continuing pattern of geographic replacement of closely related species or even what Darwin used to call "varieties." Morphological change in conjunction with the origin of new species in isolated populations—a documented phenomenon in the modern fauna, thanks to the work of Dobzhansky, Mayr and all who followed—simply must have been working as the norm throughout the history of complex life.

The section I had added to my original manuscript on the importance of considering geographic speciation when addressing evolution in the fossil record, addressed an apparent paradox: if our thesis is "true," and if phyletic gradualism in the main paints a false picture of the evolutionary process, how do we explain evolutionary trends in the fossil record—such as the net increase in brain size in hominid evolution over the past few millions of years? After all, long-term, essentially linear "orthoselection" was ruled out in our model.

That section concluded that there is a de facto pattern of net survival of some species over others (Fig. 4), based on the phenotypic properties of individuals within those species, that could well yield the trends we seem to see in the fossil record. And that, of course, was the harbinger of many debates of species selection, Vrba's (1980) "effect hypothesis," and hierarchical thinking in general.

And, sure enough, there was a big reaction to our paper—among our colleagues in the paleontological realm and, increasingly, in larger biological circles. Of course we were happy for the relatively few who congratulated us on finally bringing paleontology out of the dark ages; others said they knew it all along (which may or may not have been true)—while still others castigated us for being the ignorant renegades they took us to be.

It was Steve's final rewriting and his consistently bold rhetoric which really did the trick—in terms, at least, of commanding attention, if not universal approbation. We had posted a manifesto that could not be ignored—unlike my 1971 *Evolution* paper that had basically sunk without a trace.

At Steve's urging, we (Gould and Eldredge 1977) wrote a "where are we now?" follow-up paper five years later, publishing it in the newly-fledged journal *Paleobiology*. Steve wrote the entire manuscript, inviting me to add, delete and so forth. But all I ended up doing was sitting with him one afternoon in his motel room at yet another autumnal GSA meeting, arguing about one single—but, to my

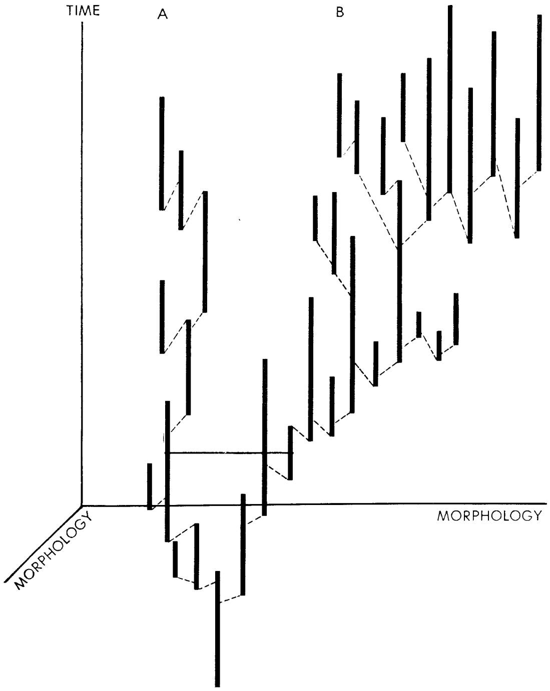

**Fig. 4** Differential production and survival of species within two related clades. Reproduced from Eldredge and Gould (1972)

mind, vital—point about the paper. Steve had used the word "tempo" a lot in the manuscript—and was in effect saying that our original paper was essentially just about variable evolutionary rates. In fact, his working title was *Punctuated Equilibria: The Tempo of Evolution Reconsidered.* I was aghast, as I had all along had George Simpson's (Simpson 1944) distinction of evolutionary tempo and evolutionary mode firmly in mind—as developed originally and best in his book *Tempo and Mode in Evolution*. Indeed, Simpson was the unacknowledged inspiration for our temerity in asserting that paleontologists looking at the fossil record could say anything original about evolution: Simpson made it clear that not all paleontological evolutionary patterns can be easily and accurately explained by simply extrapolating known genetic mechanisms (as revealed in laboratory experiments, or even in pencil-and-paper population genetics). Such patterns call for additional theory—such as Simpson had adduced in his original Quantum Evolution model for the rapid origin of higher taxa.

To Simpson, speciation is a "mode"—not a tempo. So was Quantum Evolution. I badgered Steve for what seemed like hours—and finally he agreed to add "and mode" absolutely everywhere he had written "tempo" in the manuscript—including, of course, its very title.

I tell this last story because it highlights something Steve and I said to each other periodically over the years. Steve and I, of course, agreed about most things—but so what? It was when we were disagreeing, arguing, sometimes damn near fighting—in other words, when there was half a chance you could learn something—that we were really having fun!

## 4 Postscript: On the "Deep-time" Historical Roots of Punctuated Equilibria

I feel moved to close this reflection on Steve Gould in the 1960s and 1970s, and our work together on "punctuated equilibria," with some new insights that I have been fortunate to have had recently. They concern the thoughts of the young Charles Darwin, writing his secret "*Transmutation Notebooks*" between late 1837 and 1839 (Darwin 1837–1839; see Barrett et al. 1987)—when he was between the ages of 28 and 30, ironically about the same ages that we were when were we contemplating all these issues.

Darwin, of course, was the man who, once and for all, founded the profession of evolutionary biology (not that he did not have his own predecessors—but that is another story—see Eldredge 2009). And it was Darwin who left us with the dominant picture of evolution through time as necessarily slow, steady and gradual—the result of natural selection modifying entire species as the ages roll on, and environments inevitably change.

That was the image we were criticizing—and though we have been accused of attacking a straw man of our own devising, anyone who takes a clear, objective look at Darwin's (1842) and (1844) unpublished manuscripts (C. Darwin 1842, 1844; first published by F. –F Darwin in 1909); his mid-la 1850s also unpublished "Big Species Book" (Darwin 1856–1858) to have been entitled Natural Selection; see Stauffer 1975 and, most importantly, of course, the 1859 and later editions of *On the Origin of Species* (C. Darwin 1859), will perforce agree that what Steve called "phyletic gradualism" is indeed by far the dominant view of long-term evolution that Darwin developed and left us with. And his successors more or less faithfully continued to mouth this model until Steve and I came along in the early 1970s.

But not so the young and far more interesting Charles Darwin. In my view, he can be documented (via his notes) contemplating transmutation as early as the Fall of 1832 while collecting fossils at Bahia Blanca in Argentina.

But it was only after his return home, and as an openly avowed evolutionist (if only to himself) as shown in his 1837 *Red Notebook* (Darwin 1837; see Barrett et al. 1987; Herbert 1987), that Darwin felt he had to finally confront the gorilla in the room: a natural explanation—a causal mechanism—for adaptation. Prior to that, Darwin had proceeded by adopting Brocchi's analogy: that the births and deaths of species are as much the product of natural causes as are the births and deaths of individuals. The myth that Darwin came to evolution through a theory of adaptation through natural selection is just that: a myth.

But of course adaptation is a hugely real evolutionary phenomenon. Darwin finally tackled it in his Notebook B (Barrett et al. 1987), invoking the spirit of his grandfather Erasmus' *Zoonomia* (Kohn 1987 and E. Darwin 1794–1796) for inspiration and perhaps even courage, as he took the plunge.

Darwin knew that adaptation somehow fell out of the simple fact of heredity, as well as the existence of heritable variation. But something more was needed, something was missing—and it would take Darwin another full year, and the completion of Notebooks B and C, before he found Malthus and had his 3-part syllogism of natural selection complete.

Yet, not daunted by lacking a complete and cogent mechanism for the process of adaptation in late 1837, Darwin plunged on, convinced that such a law of adaptation must exist, and determined eventually to find it (as he did a year later). The question then became—under what circumstances is that law of adaptation usually manifested?

Darwin knew—from his own data and observations gathered on the *Beagle* between 1831 and 1836—that new varieties and/or species arise in isolation—most easily seen on islands, of course, and especially on separate islands within an archipelago. The Galapagos mockingbirds are the canonical example—but he had others as well—including, as he saw it at least, the different foxes of the two main islands of the Falklands (or Malvinas). And, after he reached home in late 1836, he had plenty of other putative examples from the literature.

And, of course, such geographically disjunct and often still-isolated varieties and species are morphologically distinct—that's how you know them apart in the first place. Ergo: adaptive change occurs in isolated populations when such populations encounter new (to the ancestral species) environments—or the environments change.

In other words, Darwin knew about geographic speciation and correlated, or associated, adaptive change. It is, after all, how he came to accept the existence of transmutation in the first place.

He also knew that species have what seemed to him to have a distressing tendency to remain stable, i.e. *not* to change much if at all, through what he called "thick formations"—meaning rather long periods of geological time.

On the other hand, Darwin had a hard time imagining how isolation could happen with any degree of regularity, over the vast expanses of continental interiors—such as all of South America south of the Amazon Basin. He knew nothing of glaciation or other aspects of climate change that can partition and rearrange habitats over continental areas. And yet there were so many more species on continents than on islands and even archipelagoes!

So Darwin, without any evidence—and indeed, in spite of evidence to the contrary—began to think that this imagined black-box motor of constant evolutionary change through time must willy-nilly also account for much of the adaptive change in evolution. He became even more convinced after he nailed down his full understanding of natural selection in 1838. So gradual phyletic change was his second, rather different, model of where, when and how adaptation enters into the evolutionary picture.

And he came to see these two models—these two images of where, when and how adaptation occurs in the evolutionary process—as somehow antithetical, as alternatives to one another. To my knowledge, neither Dobzhansky or Mayr saw the two as antithetical, so we must, briefly, ask why Darwin did?

Darwin simply saw that stasis might indeed be a real phenomenon. And he also saw that geographic speciation was adequate to explain observed morphological evolutionary change in the history of life. But he could not see that it happened all that frequently—so the dominant role had to be played by something else: by his model of gradual progressive change (later modified in complex ways in his Principle of Divergence). In other words, geographic speciation could do the job if it happened regularly. And most adaptive change would happen in the brief spurts of speciation events.

And so, toward the end of Notebook E, presumably sometime in 1839, Darwin wrote the following sentence, which I personally find to be amazing:

> If separation in horizontal direction is far more important in making species, than time (as cause of change) which can hardly be believed, then, uniformity in geological formation intelligible. (Darwin 1837–1839, Notebook E, p. 135).

Allow me to translate, using the special vocabulary Steve invented to put our thoughts across in our 1972 paper:

> If separation in horizontal direction (*geographic isolation/allopatric speciation*) is far more important in making species, than time (*phyletic gradualism*) (as cause of change) which can hardly be believed, then, uniformity in geological formation (*stasis*) intelligible. (Annotated version of Darwin 1837–1839, Notebook E, p. 135).

Or, even more to the point:

> If *allopatric speciation through geographic isolation* is far more important in making species, than *phyletic gradualism* (as cause of change) which can hardly be believed, then, *stasis* intelligible. (Paraphrase of Darwin 1837–1839, Notebook E, p. 135), using Gouldian terminology,

Just exactly so! In that passage, Darwin was contrasting phyletic gradualism with the combination of geographic speciation and stasis that we called "Punctuated Equilibria."

Like Dobzhansky and Mayr before us, Steve and I had to return to the fork in the road that Darwin had encountered in the late 1830s—and, seriatim, we redeveloped and explored the path that Darwin saw but chose not to follow.

One final thought: Had Darwin seen the title of our 1972 paper—particularly when he too was a young man in the late 1830s, he would have been intrigued, but would have insisted on the simple change of but a single word: Darwin would have insisted on *Punctuated Equilibria: The Alternative to Phyletic Gradualism.*

Steve always hated to be edited—but I think in this case he would be pleased at the suggestion that ours was not just *an* alternative, but *the* alternative to the standard Darwinian image of evolution through time: phyletic gradualism.

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# Stephen J. Gould and Adaptation: San Marco 33 Years Later

**Elisabeth A. Lloyd**

**Abstract** Stephen J. Gould's concern for the wide variety of explanations for evolutionary change was one of his chief intellectual contributions. In one of his most famous papers, "The Spandrels of San Marco", named in honor of Venice's own most gloried church, and which he co-authored with Richard C. Lewontin, he emphasized the importance of historical, correlational, byproduct, and phyletic evolutionary explanations, and contrasted these with adaptationist explanations. In this Article, I take a more formal approach to discussing Gould's analysis of evolutionary explanations, now 33 years later. My analysis rests on the "logic of research questions", and contrasts a "methodological adaptationist" approach, to what I call the "evolutionary factors" approach. In the former, the key research question is: "What is the function of this trait?" while in the latter, the research question is: "what evolutionary factors account for the form and distribution of this trait?" I use my case study on the evolution of the female orgasm, which Gould defended in his column, and was one of his favorite examples, to illustrate how the methodological adaptationist approach can lead scientists astray. (Reports of a serious challenge to the byproduct account, based on recent poorly-designed twin studies, are unsupportable.) Biases induced by methodological adaptationism have led biologists to a failure to compare the byproduct hypothesis against an adaptive one with regard to the evidence. Perhaps, then, it is past time to take Gould's advice, and reevaluate whether methodological adaptationism is truly as benign as it is commonly assumed to be.

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# 1 Introduction

We do not usually think about the logic of our scientific methods leading to close-mindedness, and the inability to see alternatives, or evaluate evidence, but that's exactly what sometimes happens in evolutionary biology with one of its most popular methods, despite its benign reputation, and true to the warnings given by Stephen Jay Gould and Richard Lewontin 33 years ago in their profoundly influential paper, "The Spandrels of San Marco and the Panglossian Paradigm" (1979).

## *1.1 Adaptive Explanation*

The issues about method revolve around evolutionary adaptations, one of Evolution's biggest successes. Evolutionary adaptations are traits that exist today because they were products of natural selection acting in the past history of the species. Take the timber wolf, one of Darwin's examples. Descended from more generalized and slower carnivores, the wolf evolved specialized traits for hunting swift prey like deer and elk. There was variation in the past of the traits of speed and strength, and because there was a reproductive advantage associated with these traits, and selection for them, we have the wolf's specialized adaptations for speed and strength today. There's an important pattern manifest in the population distribution of speed in this example. In the ancestral population, speed was highly variable, with values representing the different speeds distributed widely over the population, which we can visualize as a very low or squashed bell curve, or even a flat curve. After selection has acted over evolutionary time, we have a large peak in the population distribution of speed, up at high speed. Selection processes normally produce peaks in population distributions of traits, at the value of the trait with the best fit—or closest-to-best fit—to its environment. The wolf example thus presents a good example of a natural selection explanation that produces an adaptation. Our living world is filled with examples of such adaptations.

Now, let us consider a breed of scientist called a 'methodological' or 'heuristic' adaptationist. This is an evolutionary biologist who *assumes*, at the beginning of investigation, that the trait that they are looking at is, indeed, an adaptation. As one of the founders of modern evolutionary theory, Ernst Mayr, memorably wrote, in reaction to the Spandrels paper, and in defense of an adaptationist research program, "The adaptationist question, 'What is the function of a given structure or organ?' has been for centuries the basis for every advance in physiology" (Mayr 1983, p. 153).

While this approach may look biased, since it seems that adaptive explanations would be unfairly favored, this favor is supposed to be only temporary. This more benign methodological adaptationist method has been advocated by many biologists since Mayr, and here is a philosopher's characterization of it:

> … when the hypothesis of optimality [or adaptation] is investigated first, deviation from the optimum provides evidence that other factors are at work, and perhaps the nature of the deviation will give clues about where to look next (Godfrey-Smith 2001, p. 342).

This is described as the "most helpful way to proceed"; look for a selective explanation in every case, and it might lead you to nonselective explanations, which you could then pursue if that is where the evidence led. But it is still an open question whether the method *in practice* allows non-adaptive explanations ever to win the day. Do researchers who avow such approaches in fact find themselves willing to embrace non-adaptive explanations when the evidence points toward them?

## *1.2 The Spandrels of San Marco and the Logic of Research Questions*

Problems only arise for the methodological adaptationists when a trait appears in a population that is not the direct consequence of natural selection. In Gould and Lewontin's 1979 paper, they discuss the spandrels of the church of San Marco, which are the triangular areas between the arches holding up the dome, and onto which saints have been painted, and they write that:

> … The design is so elaborate, harmonious, and purposeful, that we are tempted to view it as the starting point of any analysis… But this would invert the proper path … Yet evolutionary biologists, in their tendency to focus exclusively on immediate adaptation to local conditions, do tend to ignore architectural constraints and perform just such an inversion of explanation (Gould and Lewontin 1979, pp. 79–82).

In their paper, Gould and Lewontin emphasize a basic fact of evolution, namely, that not every biological character is adaptive, and that there exist alternative evolutionary explanations available and sometimes appropriate, such as evolutionary developmental accounts, architectural byproduct accounts, accounts that cite correlations of growth, and so on. But they emphasize that there is an important difference between paying lip service to this view, and using this theoretical assumption in actual research.

Now, later in history, we are in a position to see a clear contrast between two distinct methodologies and corresponding sets of questions. And we know that different questions make different answers legitimate. I call this the 'Logic of Research Questions'. The logic of the research question we ask constrains what type of answers we can give, so we need to think very hard about the research questions we ask, because the questions can lead us to actually miss what's really going on, and therefore to scientific failure.

The methodological adaptationist asks, echoing Mayr's rebuttal to Gould and Lewontin, "what is the function of this trait?" And there are any number of possible answers to this question, which take the form:

*Possible Answers:*

A: The function of this trait is B
A: The function of this trait is C
Etc.

I characterize an alternative approach here, as the ‘evolutionary factors’ approach, whose research question is: “What evolutionary factors account for the form and distribution of this trait?” And it has a series of possible answers, including:

*Possible Answers:*

A: This trait occurs in the population because it has the function B, which is an adaptation
A: This trait occurs widely in this population because it is genetically linked to a trait that is highly adaptive in this species
A: This trait has its current form largely because of an ancestral developmental pattern.
Etc.

Note that the first answer is an adaptation answer, which suggests that adaptation is also explored, as a priority, in the evolutionary factors approach.

## 2 Case Study: The Evolution of the Female Orgasm

Let us turn to a case study in the logic of research questions—it is a provocative and interesting case study, but please do not lose sight of the fact that it is only a case study, and not itself the point of the paper.

I use my case study on the Evolution of the female orgasm, which Gould wrote about and defended in his column in *Natural History* magazine—in fact, it was one of his favorite examples of an evolutionary developmental byproduct—to illustrate and confirm how the methodological adaptationist approach can lead scientists astray (Gould 1987).

I should say at the start that reports of the demise of the byproduct account of female orgasm are greatly exaggerated. A recent twin study by Zietsch and Santtila claimed to have undermined the byproduct account (2011). They first said that the byproduct account predicted that what they called “orgasmic function” should be correlated in male and female twins. But their twin study showed that it was not correlated. The chief and fatal problem with the study is that the traits studied under the name “orgasmic function” were hopelessly different: they counted the time to orgasm in men, that is, the time it takes for a man to have orgasm once he starts copulation, and compared it to a completely different measure in women, whether or not she has orgasm at all (2011, p. 1098). As you can see, these two traits are quite distinct, and would not be expected to correlate, in any case. Thus, the lack of correlation of these two traits that Zietsch and Santtila found was to be expected, and says nothing against the byproduct view, contrary to their claim (2011, p. 1100; Wallen et al. 2012).

In my book published in 2005, *The Case of the Female Orgasm*, and quickly translated into Italian (2006), I gave detailed examinations of all 21 published theories of how female orgasm had evolved; 20 of them claimed that orgasm was an evolutionary adaptation. With the wolf case, we saw an important kind of evidence that is at stake when evolutionists consider an adaptive account of a trait. That is, directional selection produces a peak somewhere in the distribution of the trait in the population; the same is true of stabilizing selection, the type of selection (on males) involved in the byproduct account. Now contrast the peak at high speed in the population distribution of wolves with the distribution we find of orgasmic performance among women (Fig. 1).

Note that only about 13 % of women always have orgasm from intercourse, and roughly a third of women rarely or never have orgasm with intercourse in their whole lives. In Dawood et al.'s data, 13 % of women never have orgasm at all from any means (2005). These data are consistent with the results from the 35 studies I analyze in my book (2005), and also a more recent, large twin study (Dunn et al. 2005). As you can see, this curve is basically flat. Simple selective forces produce peaks in the distribution curves of a trait, as more and more of the organisms in a population are selected to have the desirable form of the trait. All except one of the proposed selective explanations for female orgasm predicts a peak in this curve, but there are no peaks. Hence, all but one of the selective and adaptive explanations for female orgasm is undermined by these data from sexology.

There is another way in which all of the adaptive explanations, including the Female choice theory, are undermined by sexology data, as well. Zietsch and colleagues (2011) examined correlations of such potentially adaptive traits and orgasmic activity in a population of nearly 3,000 women, finding zero to very weak correlations across all 19 traits they examined including libido, social class, orientation toward uncommitted sex, restrictive attitudes towards sex, lifetime number of sex partners, and so on. None of the correlations had significant genetic

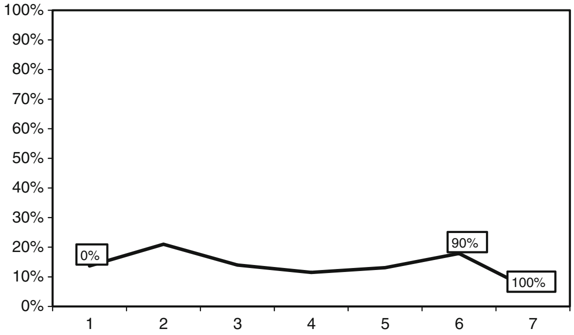

**Fig. 1** The x-axis represents overall orgasmic performance with heterosexual vaginal intercourse, while the y-axis represents frequency in the population. Constructed from Dawood et al. (2005)

components, thus undercutting any ascription of a fitness benefit to orgasm. In addition, there has never been any evidence linking orgasm to fitness or number of babies, frequency of intercourse, or any other trait correlated to fitness, and this new study echoes this very significant lack (Bancroft 1989). In other words, having orgasms is not associated with having more or better babies, the very basis of selective change.

## *2.1 The Fantastico Bonus Account (Aka Byproduct Account)*

Now, I would like you to consider the problem of why male mammals have nipples. Nipples clearly provide a reproductive advantage to female mammals by providing the means to feed the offspring; they have an evolutionary function. But there is no known contribution to fitness, or function, for the males.

The evolutionary explanation for the existence of male nipples is a non-adaptive one in the males, based on the development of the embryo. Males and females share the same embryological form at the beginnings of life; they start off with the same basic body plan, and only if the (chromosomally male) embryos receive a heavy dose of hormones during the 8th week of pregnancy do any sexually distinguishing characteristics appear. In females, nipples are adaptations—they were actively selected for—but the males get them for free. This sort of explanation is a 'developmental' or 'non-adaptive' one—male nipples are seen as evolutionary byproducts, with no function of their own.

A parallel explanation was offered, by anthropologist Donald Symons, back in 1979, for the female orgasm. Females have orgasm because orgasm is strongly selected in males, and both sexes share the common form in the womb. The tissues involved in orgasm for males and females are homologues, including nerve tissues, erectile tissues, and muscle fibers. Thus, females get the orgasmic tissues through this embryological connection and are often capable of having orgasms under the right conditions of rhythmic stimulation.

There is a variety of evidence supporting this byproduct account of female orgasm, although it has encountered a great deal of resistance. Part of this is surely the "byproduct" name, which many women find demeaning. So I'm in the process of renaming it the "fantastico bonus" account, which is much more accurate, after all.

Symons's account accords well with the data available about human female sexuality. Women do not masturbate by simulating intercourse, that is, solely by vaginal insertion, they do it by stimulating the clitoris directly or indirectly (Kinsey et al. 1953). Men masturbate the same way, by stimulating the homologous organ.

Ten of the adaptive accounts assume that women virtually automatically have orgasm with intercourse, the way men do, and when faced with the real sex evidence, they cannot account for the lack of orgasmic frequency (Lloyd 2005). The byproduct theory, though, allows us to make sense of the infrequency with which women experience orgasm with reproductive sex.

Symons's general thesis is also supported by the nonhuman primate evidence, which shows, among other things, that female stumptail macaques have the distinctive contractions and other bodily markers characteristic of orgasm.

Note that Symons and I are not denying that the *clitoris*, as an organ of sensation, almost certainly has been selected because it aids the female in sexual excitement and induces and prepares her to seek out and have intercourse. But this reasoning does not extend to the use of these same tissues for female orgasm. Orgasm is a special reflex that sometimes results from clitoral and genital excitement. Now it is time to consider the female choice type of sexual selection hypothesis, which is the only adaptive hypothesis on offer compatible with the wide variability of orgasmic experience in women, which shows up as the flat curve of orgasmic distribution.

## *2.2 Female Choice Hypothesis and the Uterine Upsuck Account*

The basic idea of the female choice hypothesis offered for female orgasm is that the female will mate with more than one male over either a short period of time, or over different cycles, and have orgasm preferentially with the higher-quality males. These theorists assume that orgasm is accompanied by a mechanism of uterine upsuck that makes it more likely that the female will be fertilized by the higher quality male. Thus, the orgasmic women are required to respond with orgasms only sometimes with intercourse—yes with high quality males, and no with lower quality males (Thornhill et al. 1995; Hosken 2008; Puts et al. 2012). This type of female choice selection can theoretically produce the flat curve of wide orgasm variation, but only provided that the force of selection is strong. Specifically, note that Hosken (2008) appeals to the population genetics models of Pomiankowski and Møller (1995) to produce wide variation, and those models require strong selection. Thornhill et al. (1995) and Puts et al. (2012) produce no selection dynamics with their account, but something like the available female choice genetic models would be required to produce the present variation.

But consider what is needed to fulfill this female choice model. It requires multiple mating by women before insemination. How many women fulfill this in a given population, and how strong a selection pressure can this be, also given that selection on one sex is only half as strong as selection on both? The fitness effect in the selection scenario proposed depends on indirect selection on female orgasm arising from a difference in offspring quality, not quantity, given the opportunity to choose by multiple mating. All this is extremely unlikely to add up to the strong sexual selection required, in order to explain the very high level of phenotypic variation of orgasm. But now there is a new challenge to this model.

In a new study published by neurophysiologist Kim Wallen and I (2011; see Fig. 2), those women who reported orgasm with intercourse (white bars) had

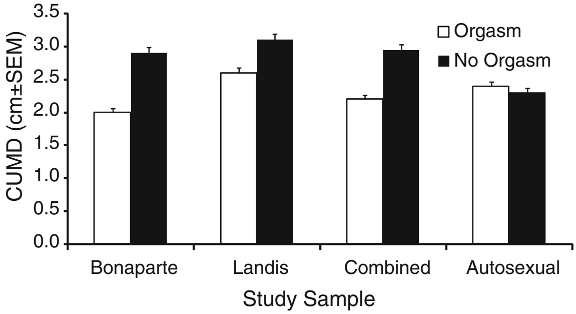

**Fig. 2** Average Clitoral-Urinary-Meatus-Distance (CUMD) measurements in the Landis and Bonaparte samples, for those women routinely experiencing orgasm in intercourse (66 % of the time or more, *white bars*) and those not (*black bars*). Data are shown for the samples combined, and for the Bonaparte sample's masturbatory (autosexual) orgasms, as well. Data are all statistically significant, except for the difference in the two autosexual samples

significantly shorter distances between their clitoris and their urinary opening, which appears in Fig. 2 as CUMD, than did women who did not report orgasm with intercourse (black bars). We found this strong correlation in two distinct datasets, Bonapart and Landis, and the difference was highly statistically significant—over two standard deviations, with an *r* of 0.6 in the combined dataset. We also found that this anatomical distance was strongly *predictive* of whether a woman had orgasm with intercourse. This distance is irrelevant to orgasm with masturbation, as we would expect.

In other words, we found that an anatomical trait, basically this distance between the clitoris and a structure near the vagina, strongly predicted whether or not a woman would have orgasm with intercourse or not. If you think about it, this makes good sense. The further away the clitoris is from the vagina, the less likely it is that she will have an orgasm with intercourse, possibly because her clitoris is not being stimulated enough by the activities going on around the vagina. Clearly, if her anatomy so strongly influences whether or not she has an orgasm with intercourse with a male, that leaves little room for the genetic quality of the male to also strongly influence the outcome of such intercourse. Again, according to the theorists, the selection pressure of this type of selection scenario needs to be quite strong in order to produce any result in terms of evolution. Puts et al. (2012) characterize the anatomical trait and relation we discovered as an aspect of the environment in which female choice evolved, but it seems that our strong correlations make such a scenario quite unlikely.

Overlooking for now the substantial hurdles embodied by this evidence, female choice theory can only work if there is a physiological relation between female orgasm and fecundity, a mechanism that is usually simply assumed. The hypothesis had achieved widespread acceptance since the nineties through the work of Robin Baker and Mark Bellis. But examine their data. In one data set, they have 1 out of 11 couples in the sample contributing 93 out of the 127 data points (nearly three quarters of the data). 4 of the other 10 couples contributed one data point each, a combined total of 3 % of the data, and so on (Baker and Bellis 1993; see Lloyd (2005) for much more analysis of problems with their statistics). But extrapolating to the population at large based primarily on the results of a single subject badly violates standard statistical practice. In the end, the Baker and Bellis data are statistically worthless and no scientific conclusions can be drawn from them.

But many dozens and even hundreds of adaptationists nevertheless used this paper to support their desired conclusion that female orgasm was an adaptation, and used it directly against the viability of the byproduct account, despite its obvious flaws (e.g., Alcock 1998). The human evolution field's instant acceptance of the Baker and Bellis paper, and its continuing use of the paper in lectures and teaching, as well as research, was an example of adaptationist bias getting the better of scientific judgment or the application of normal statistical standards. Adaptationist bias consists in favoring adaptive accounts over the nonadaptive accounts without good evidence for doing so, or, indeed, against the evidence.

Nowadays, the favorite mechanism for the preferential movement of sperm of the superior male is the effects of oxytocin (Puts et al. 2012). But those experiments used a dose of 400 times the actual level released during orgasm, and are thus irrelevant to the biological question without further research (Levin 2011). So both theoretically and empirically, the female choice hypothesis is facing very substantial hurdles before it could be accepted as a plausible theory of female orgasm. The byproduct hypothesis, on the other hand, has much evidence supporting it. So how are the two evaluated and compared by biologists? Here's where the biases, and above all, methods, really play a central role.

## 3 Analysis of Methodological Adaptationist Approach Versus Evolutionary Factors Approach

When a methodological adaptationist does research, and asks their key question, "what is the function of female orgasm?", the assumption is that selection brought the orgasmic structures to their present state; the problem or challenge is to figure out which selective hypothesis is correct. So far, we have:
*Possible Answers:*

A: The function of this trait is to cement the pair bond
A: The function of this trait is to aid in preferential insemination by high-quality males.

But where does the byproduct hypothesis belong? Some of the adaptationists in this case see the byproduct view as a sort of "null" hypothesis. In general usage in science or biology, a null hypothesis is usually a negative alternative to a positive correlational hypothesis. The positive hypothesis would be one in which a trait was positively correlated with fitness or some component of fitness, while a null hypothesis would be simply the non-correlation with fitness, indicating non-selection. So, on this characterization, the answer would be:

A: The trait is a byproduct of selection on males, and has *no function* in females.

They often call this a "null" result.

For a methodological adaptationist, the non-selective hypothesis is often treated as the failure to find an explanation, which they view as akin to scientific surrender (Alcock 1987, 1998; Sherman 1989). It's not seen as a positive explanation—in fact, the byproduct explanation is seen as no explanation at all. This is at least partly because it cannot be an answer to our adaptive question, it is *nonresponsive*.

On leading animal behaviorists John Alcock's and Paul Sherman's analysis, the byproduct hypothesis is a null result, and offers only a "proximate" explanation of how women come to have orgasms. In other words, it explains how female babies grow up to have orgasms as adult women, but does not offer an evolutionary account. But Alcock writes that

> If we were to discover the female orgasm occurred with positive effects on female reproductive success, we would gain an *evolutionary* dimension to our understanding of this trait that is not covered by *any* proximate explanation (emphasis mine, emphasis his, Alcock 1998, p. 330).

Thus, the byproduct account is not seen as an evolutionary account at all—it is not an answer to any evolutionary question about female orgasm, with its own supporting evidence and theoretical standing. Alcock and Sherman treat it as a failure of *evolutionary* explanation altogether. And this is clearly a result of the fact that the only answer to their adaptation question had to do with describing a function for female orgasm. With no reproductive function, the orgasm is seen as having no evolutionary role at all. This is a consequence of the logic of the research question.

Similarly, David Barash, the author of the most widely selling textbook on sociobiology for a couple of decades, and a grandfather of the field of human evolution, writes, with his wife, regarding the impetus behind those favoring the byproduct theory, that it involves

> a scientifically legitimate desire to explore all possible explanations for any biological enigma of this sort, including the 'null hypothesis' that it might not be a direct product of *evolution* after all (Barash and Lipton 2009, p. 133; my emphasis).

And here, note the equivalence of evolution with selection in this statement; the byproduct explanation is mistakenly not considered evolutionary, just as we saw before with Alcock and Sherman.

So here we have the situation: we ask the Methodological Adaptationist Question:

"what is the function of the female orgasm?" And we consider and test the appropriate answers.

*Possible Answers:*

A: The function of this trait is B
A: The function of this trait is C
Etc.

But with too many failures, we get what they call the "null" result: That the trait has no function in females. They conclude "it may not be a direct product of evolution at all." We should correct this answer to: "it may not be a direct product of selection at all." So, the byproduct answer seems to be, for them:

A: null result: the trait has no known function or correlation with fitness, and may not be a direct product of selection at all.

But we should consider the positive alternative:

A: The trait is a byproduct of selection on males, and has no function in females.

Note that in both cases, there is *no function* in females, which is *still nonresponsive* to the research question of the methodological adaptationists, because it requests a function. Instead, Symons' byproduct explanation should be seen in terms of the logic of the evolutionary factors research question, specifically, "what evolutionary factors account for the form and distribution of the trait of female orgasm?"

*Possible answer:*

A: This trait has its current form and distribution largely because it is a byproduct of strong stabilizing selection on the male orgasm. (This is the correct reading of the byproduct theory, a positive alternative causal hypothesis.)

Contrast this answer with the characterization of the byproduct view offered under the methodological adaptationist research method:

*Possible answer:*

A: This trait has no known function or correlation with fitness, and may not be a direct product of selection at all (what adaptationists call the "null" hypothesis, which they think is equal to the byproduct hypothesis).

Hence, the methodological adaptationists' portrayal of the byproduct hypothesis is misleading, and in fact, incorrect. When the byproduct hypothesis is treated as merely a non-answer to the adaptive evolutionary question asked, it also cannot be seen as accumulating evidence in its favor. As an answer to the more inclusive evolutionary factors question, the byproduct account is an alternate causal hypothesis to an adaptive account, with a set of specific evolutionary mechanisms involving indirect selection, which can accumulate evidence in its favor: it is not merely a null result. Thus, even though the methodological adaptationists present their adherence to their research program and its attendant question as perfectly harmless and in fact very good and productive science, we can see here, exactly, where it goes astray.

In essence, the byproduct hypothesis *cannot* be an answer to the function question, while it is a perfectly acceptable answer to the evolutionary factors question. We can see in these various researchers' responses to the orgasm case how confused they become by focusing only on their primary research question. For example, when a group of adaptationists were launching arguments against Gould's presentation of Symons's byproduct hypothesis that was based on my analysis, they—very strangely—behaved as if no empirical evidence had been considered at all. Adaptationist Donald Dewsbury, a very distinguished psychologist studying animal reproductive behavior, for example, claimed in response to Gould's discussions that

> … we need to study the consequences of orgasm for differential reproductive success and then determine whether a plausible case can be made for drawing the loop from present consequences to the past history of natural selection. These need to be studied, *not asserted or denied* a priori (Dewsbury 1992, p. 103; my emphasis).

The perception was, clearly, that no good evidence had entered into the debate, despite Symons's entire chapter in 1979 detailing evidence supporting his theory, and Gould's appeals to the 66 years of sexology evidence, and so on. But since all of that evidence seemed to favor the byproduct view, a theory that was considered only a null account, it was invisible to these researchers. This is where the logic of research questions really does its damage.

Gould and Lewontin complained in their spandrels paper that if one selectionist explanation failed to explain the trait under investigation, the adaptationists would simply turn to another adaptationist explanation, and then another and another; there seemed no end of selection hypotheses that could be appealed to. In essence, there is no stopping rule for the research question, "what is the function of this trait?" As a result, the lack of evidence favoring all the hypotheses proposed so far for a trait is rightly perceived as no impediment for its future success as an adaptation of some sort; thus, the so-called "null" hypothesis, or no-function view of the byproduct hypothesis is neither attractive nor needed, since a new function story is always available. Note that the repeated failure of adaptationist accounts does not have any bearing on the positive evidence available supporting the byproduct account, although many adaptationists incorrectly believe that this is the sole evidence supporting the account (e.g. Alcock 1998; Lindquist 2006). Because the logic of the function question demands a function answer, no byproduct answer can be considered a positive answer to the research question, and thus have support in its favor, and we do find the participants in the debates following this logic.

On the logic of research questions, though, the evolutionary factors approach works very differently from the methodological adaptationist one in terms of how to treat evidence: an adaptive hypothesis can be compared directly to a non-adaptive, byproduct theory, by comparing evidence in favor of each view. As we saw, under the function question, the byproduct account gets incorrectly classified as a null hypothesis, and a null hypothesis cannot have independent evidence in its favor. But the methodological adaptationists never get a chance to compare the byproduct hypothesis as a positive causal hypothesis because they have no stopping rule, and would have to give up on their quest for a functional hypothesis, at least temporarily, and switch questions to the evolutionary factors approach. No researcher opposed to the byproduct account involved in this debate has ever done this, at least in print. Compare the two questions and their samples of relevant well-formed answers here:

What is the function of this trait*?*
*Possible Answers:*

A: The function of this trait is B
A: The function of this trait is C
A: The function of this trait is D, or E, F.…Z, AA, BB,.…ZZ, AAA, BBB…????
[Faulty A: This trait has no known function or correlation with fitness, and may not be a direct product of selection at all (what adaptationists call the "null" hypothesis, which they think, falsely, is equal to the byproduct hypothesis)]
Etc.

What evolutionary factors account for the form and distribution of this trait?
*Possible Answers:*

A: This trait occurs in the population because it has the function B, which is an adaptation
A: This trait has its current form and distribution among one sex largely because it is a byproduct of selection on the opposite sex's trait
A: This trait occurs widely in this population because it is genetically linked to a trait that is highly adaptive in this species
A: This trait has its current form largely because of an ancestral developmental pattern.
Etc.

Under the logic of research questions, then, those using the methodological adaptationist approach cannot adequately evaluate the accumulated evidence for the byproduct approach. This evidence is in some sense only visible on the evolutionary factors approach, where the weight of evidence is the right rule to use in evaluating the byproduct hypothesis and its alternatives.

The methodological adaptationists also make basic scientific errors arising from their method. For example, several adaptationists repeatedly complain that under the byproduct hypothesis, female orgasm would fade away and deteriorate over evolutionary time, and would tend to disappear from the population. This notion has been advanced not only by leading scientists such as Alcock, Sherman, and Barash, but also by outstanding primatologist and human evolutionist Sarah Blaffer Hrdy, and it is based on a misunderstanding of how the byproduct account works (Alcock 1998; Sherman 1989; Smith 2005). This misunderstanding is likely a consequence of their adaptationist bias that a particular trait will only be sustained in a population if it itself is under sustained selective pressure. But under the byproduct account, the basic muscle, nerve, and tissue pathways involved in female orgasm would be maintained in the female over the generations in virtue of the fact that they are under ongoing strong selection in the male. Thus, methodological adaptationist explanatory biases have led to fundamental mischaracterizations of the byproduct hypothesis.

## 4 Conclusions

In conclusion, Gould's approach to evolutionary biology says that we should not privilege adaptation explanations automatically above other alternatives, such as developmental or phyletic ones, and our research methods should not bias our research outcomes. This is among the main messages of Gould and Lewontin's famous spandrels paper, which most biologists say is now passé, and claim that biologists simply do not make those mistakes any more, if they ever did. This is clearly false, as we can see from this problematic case. Even in the most recent discussions in the orgasm controversy, the philosophical, theoretical and evidential issues are unresolved. And I would like to emphasize that I am not in any way against adaptationist explanations themselves. In fact, I think that the first type of explanations that should be considered using the evolutionary factors approach are adaptationist ones; we should start our examination of any trait by asking whether it is adaptive. But I am using this case to highlight some *risks* of a particular approach to research into evolutionary causes. These risks become obvious when we examine the logic of the research questions and their relevant answers, within the methodological adaptationist approach. When a research method makes any particular types of hypothesis especially difficult to entertain or accept, it deserves serious scrutiny. The presence of researchers like Symons who engaged in their research using the more inclusive evolutionary factors approach exemplify an available alternative method. Evolutionists all say that they have learned their lessons about an inclusive approach to evolutionary explanation from Gould and Lewontin's 1979 spandrels article, but methodological adaptationism seems to make it very difficult for them to act on those lessons. Grazie molto.

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# Kinds of Pluralism: Stephen J. Gould and the Future of Evolutionary Theory

**Telmo Pievani**

**Abstract** Stephen J. Gould's living legacy is a scientific and epistemological one, much beyond his talent as science writer and communicator in evolutionary topics. In the XX century Gould has been one of the most important evolutionary biologists proposing a new logical and theoretical "structure" for the whole theory of evolution, not just a description of disjointed innovative emerging fields. He named this structure "Darwinian pluralism" or extended Darwinism. Ten years after his death and after a lot of impressing new discoveries in many evolutionary fields, we discuss the efficacy and limits of his pluralism, also in comparison with other kinds of pluralistic approaches to the units, the levels and the factors of evolutionary change. Adopting the methodology of "scientific research programmes", we present Gould's legacy as a peculiar expression of reformist Neo-Darwinism: polemic targets are referred to the so called "hardenings" of the Modern Synthesis, whereas the assumptions of compatibility are referred to the core of the original Darwinian theory.

## 1 Introduction

Evolutionary biology is a rapidly evolving subject. At an accelerated pace, we are confronting uproarious advances in several fields like genomics (see for example "Encode" programme about the non-coding sequences of DNA, or recent discoveries about RNA machinery), lateral gene transfer, symbiosis, epigenetics, evolutionary developmental biology, new comparative studies, macroevolutionary patterns such as mass-extinctions, and so on. These wide and diversified domains of research have both experimental and theoretical impacts: they both enlarge

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additively the empirical basis of the theory of evolution in unpredictable ways and redefine concepts and terms. Ranging from ecology to molecular biology, they change evolutionary biology at different levels of analysis, from global ecosystems to the biochemistry of life. It is unlikely that all these progresses will not have an impact on the structure of evolutionary theory itself, which is not the same as decades ago.

The revision and extension of evolutionary theory was one of the main interests of Stephen J. Gould (hereafter: SJG), and for many reasons the core of his intellectual legacy. As first thesis of this paper, in terms of theoretical biology, we will point out that SJG did not have an additive and purely descriptive conception of these advances. In order to build a somehow "Extended Evolutionary Synthesis", he thought that it was not enough to enucleate the more innovative emerging fields (like the conjunction of phylogeny and embryogenesis foretold by him very early in 1977 with *Ontogeny and Phylogeny* 1977a) and sum up the updating lines as a list of disconnected topics. In the XX century SJG was one of the most important evolutionary biologists proposing a new logical and theoretical "structure" for the whole theory of evolution. He named this structure "Darwinian pluralism" or extended Darwinism. Up to now, there are few other attempts with a similar ambitious scope. Thus, ten years after his death and after a lot of further impressing discoveries, it could be interesting to discuss the efficacy and limits of his pluralism.

A collateral question is steadily emerging, not so crucial in a scientific sense but very overexposed in mass media: is this new structure still Darwinian or "Neo-Darwinian"? (in an extended meaning of the latter term, as redefinition in modern scientific language of the core of Modern Synthesis). The answer to this question (our second thesis here: SJG as a peculiar expression of reformist Neo-Darwinism) leads to a contentious theme for the future. Are these extensions so huge and radical that there is no more a "theory of evolution", but just a collection of mechanisms and data searching for coherence? Or is a new structured theory emerging? In order to reach a consensus about that, maybe the narrow term "theory" should be replaced by the more articulated epistemological tool proposed by Imre Lakatos for other disciplines: evolutionary biology today has something more than a theory, it has a "research programme" (Lakatos 1978; Pievani 2012a).

Is this research programme progressive (outwards empirically successful and inwards theoretically consistent) or regressive (accumulating anomalies)? Has SJG well interpreted the extensions and revisions needed? Focusing on his idea of "hierarchy" of selection units, we could surprisingly discover that SJG was for some aspects conservative, and that other kinds of pluralism could be even more far reaching. SJG's pluralism should be intended as an agenda for future extensions and revisions of the evolutionary research programme: in many cases his predictions have been confirmed (an outstanding example: in paleo-anthropology) whereas in other cases they failed. Anyway, it should be acknowledged that SJG's living legacy is a scientific and epistemological one, much beyond his talent as science writer and communicator in evolutionary topics.

## 2 Stephen J. Gould's Pluralism

The heritage of such a polymorphic and productive scientist needs to be studied with careful methodological principles, in order to correctly analyze his vast production. SJG is known for his political and sociological thought (Prindle 2009), his style of communication and writing (Selzer 1993), his famous public controversies and intellectual provocations (Sterelny 2001), his role as a historian and philosopher of science, his ability to write remarkable works on the history of science based on primary sources. Thus, his influence was in many cases indirect. Let us take the case of human evolution (discussed in: Pievani 2012b). As an invertebrate paleontologist and evolutionary theorist, SJG did not publish any direct experimental results in palaeo-anthropology (with the exception of Pilbeam and Gould 1974), but was able to prepare the stage for many debates within the discipline, frequently concerning some implicit, powerful but misleading concepts applied to human evolution.

As for strictly technical contributions in formal palaeo-anthropological literature, Michael Shermer quantified 13 publications in the huge amount of SJG's technical papers (479) (Shermer 2002). The role of SJG's ideas in paleo-anthropology is an example of indirect, successful theoretical influence between a general scientific "research programme"—that is evolutionary thought at large—and one of its strikingly changing sub-fields, the study of human evolution (see also Tattersall 2013). Though indirectly, SJG was able to anticipate some meaningful scientific predictions, i.e. the branching richness of the "bushy tree" of hominin phylogeny or the role of neoteny in *Homo sapiens* evolution (Gould 1980, 1989). A similar case could be sketched out about the mass-extinctions debate and SJG's contribution to the revival of scientific "Neo-catastrophism" (Gould 1985; Benton 2003).

The scientific and epistemological production of this eminent Harvard evolutionist was very heterogeneous as well. The proposal of an extended and revised Darwinism was outlined mainly in the last twenty years of his life (1982–2002) and depicted in his monumental work, *The Structure of Evolutionary Theory* (2002a). In order to detail the structure of his extended theory of evolution we need to consider the two collective books dedicated to him after his death: Vrba and Eldredge (2005) and Allmon et al. (2009). The latter presents the first apparently complete bibliography of Gould's work, compiled by Warren D. Allmon: 814 titles. Furthermore, we have to consider his famous series of three hundred popular essays in *Natural History* magazine, carefully gathered in ten volumes (for an essential compendium: McGarr and Rose 2006).

One of SJG's preferred methods was the extraction of "general themes" of evolutionary thinking from idiosyncratic stories, seemingly insignificant details and marginal actors of the history of science (Gould 2002b). Surveying his writings, we could use the same criterion for an evaluation of the whole structure of his lifelong work, which includes 22 books (with the two most technical at the very beginning, *Ontogeny and Phylogeny*, 1977a and at the end, *The Structure of*

*Evolutionary Theory* 2002a), 479 scientific papers, 300 essays in the *Natural History* magazine, and dozens of other articles and reviews.

Organizing the huge material by conceptual themes, we propose to divide SJG's pluralism in three main fields, each one with a main topic, sub-fields, and more general philosophical consequences (see Table 1). Each domain has also its specific polemic targets, because SJG always followed one of his preferred Darwin's epistemological quotations. In a letter to Henry Fawcett two years after the publication of the *Origin*, the great naturalist, counterbalancing his typical inductivism as a methodological background, wrote: "All observation must be for or against some view if it is to be of any service" (Darwin to H. Fawcett, 18 September 1861; see www.darwinproject.ac.uk). In Imre Lakatos' modern terminology, any scientific research programme must be evaluated in comparison with at least one other rival programme (Lakatos and Musgrave 1974). SJG loved what Gerald Holton defined antagonistic themata or "thematic pairs" in science: gradualism/punctuationism; holism/reductionism; time's arrow/time's cycle; adaptationism/non-adaptationism; contingency/necessity; theory/data (Sulloway 1987).

But each domain has also assumptions of compatibility, because SJG's overall proposal is a kind of inclusive pluralism with respect to the Neo-Darwinian tradition of research. As we shall see, polemic targets and thematic pairs are referred to the so called "hardenings" of the Modern Synthesis, whereas the assumptions of compatibility are referred to the core of the Darwinian theory. In those thematic pairs, as SJG's favourite conclusion claims, not everything can be explained by just one horn of the dilemma.

The structure of SJG's pluralism is seen here in a synoptic way (see Table 1). He wrote 136 peer-reviewed papers about evolutionary theory, 64 about natural history (zoology, biology and environment) and 115 about paleontology and paleobiology (including Punctuated Equilibria, paleo-anthropology and geology). An analogous blending of themes emerges from statistics applied to his 300 essays in *Natural History* (the first one, in January 1974, was about "Size and Shape") (Shermer 2002). The same impression of integration arises from a diachronic sketch of the whole scientific production of the Harvard paleontologist (see scheme 1 in Pievani 2012b, pp. 2–3): with the early technical studies about allometry, shape and size in West Indian land snails (since Gould 1966), the strongly debated Punctuated Equilibria initial paper (Eldredge and Gould 1972), and the first essays against genetic extrapolationism and biological determinism (Gould 1977b). This scheme aims at putting SJG's work in a larger and consistent context, which stresses the global integration of his theoretical heritage. His writings are neither a collection of separated topics, nor a list of weird evolutionary stories. They have a visible frame, a pluralistic research programme. The same property has been highlighted by Michael Shermer in the interconnections of subjects throughout the broader SJG's interests in history of science, science studies, philosophy of science and evolutionary researches (Shermer 2002).

**Table 1** Sketch of SJG's pluralistic and extended Darwinism (for the numbers of publications by categories: Shermer 2002)

| SJG's Pluralism (A + B + C) | Main topics | Sub-fields | Greater philosophical consequences | Polemic targets | Assumptions of compatibility |
|---|---|---|---|---|---|
| **A**—Plurality of rhythms of speciation and rates of evolution | **Punctuated Equilibria** (three patterns: stasis, allopatric and geographic speciation, evolutionary trend; see Eldredge, 2013)<br>15 papers on the subject (+5 popular essays) | (1) Biological definition of "species" as an ontological discrete entity<br>(2) "Punctuational" phylogenetic trees<br>(3) Differential mutational rates<br>(4) Mass-extinctions as independent macro-evolutionary pattern<br>(5) Experimentation—standardization model (Burgess Shale case)<br>(6) Role of the ecological opportunities | Evolution as an irreversible process of exploration of possibilities<br>The role of chance in evolution<br>"Punctuational" extended thinking (in SJG, not the same in Eldredge) | Phyletic gradualism (44 essays)<br>Uniformitarianism<br>Progressionism | Slow processes of speciation not excluded (debate about their relative frequency in natural history)<br>Gradualistic patterns (and trends) in natural history not excluded (but explained at a higher level of biological organization as differential survival of species) |
| **B**—Plurality of units of selection | **Hierarchical levels of selection** (as a macroevolutionary extension of Punctuated Equilibria) | (1) Species as units of evolutionary change<br>(2) Hierarchy of levels between micro-evolution and macroevolution: each level with emerging properties due to the organization of the parts<br>(3) Between hierarchical levels, interactions bottom-up (standard) and top-down (inaccurately defined in SJG)<br>(4) Slippery concepts of biological "individuality" (continuity in nature) (see Minelli 2013)<br>(5) Genome itself as a hierarchical system<br>(6) Possibility of selective processes at the gene level<br>(7) Group selection;<br>(8) Species selection and "species sorting" | Macroevolution cannot be linearly extrapolated by microevolution as an accumulation of effects at lower levels<br>Emerging patterns at higher levels | Extrapolationism<br>Genetic determinism | Standard natural selection acting on organisms still crucial.<br>Selective processes, at any level, not excluded |

(continued)

**Table 1** (continued)

| SJG's Pluralism (A + B + C) | Main topics | Sub-fields | Greater philosophical consequences | Polemic targets | Assumptions of compatibility |
|---|---|---|---|---|---|
| **C**—Plurality of factors and processes able to produce fitness | **Exaptation** (functional cooption from previous adaptation)<br>and<br>**spandrels** (non adaptive traits and functional cooption from non-adaptations)<br>(the two concepts are different) | (1) Biased variation<br>(2) Constraints and limits of natural selection<br>(3) Interplays between functions and structures, internal factors and external factors<br>(4) Structural changes, allometric constraints and forms in evolution<br>(5) Organisms as integrated units<br>(6) Positive causal role of constraints (developmental, physical)<br>(7) Multiple sources of variation and innovation (genetic, epigenetic, developmental)<br>(8) Adaptation as a constrained, sub-optimal solution for a selective pressure<br>(9) Phylogenetic ancestry does not mean primitive adaptations<br>(10) The role of plasticity (at different levels) in biological evolution | Join together the structuralist and the functionalist traditions in biological thought (76 essays)<br>Disaggregate historical origin and current utility<br>Time's arrow and time's cycle (80 essays and a book, from 1965 to 1987) | Biological atomism<br>Pan-selectionism<br>Strong adaptationism<br>Strict functionalism | Standard adaptations by natural selection still included:<br>extended taxonomy of fitness (adaptations, exaptations, spandrels) |

## 3 His Way to Be a Darwinian

Summing up the three great domains of his pluralism, we understand SJG's apical view of the "nature of history" (Sulloway 1987). Evolution is an irreversible process, with its specific historical patterns. As SJG repeated, history matters (Gould 1987) and after Darwin natural history has acquired a scientific status for the first time. Here we appreciate the everlasting dialectic that SJG engaged with the founding father of the theory of evolution by natural selection. It was a scientific, historical and epistemological man-to-man fight, with strong attractions and repulsions. Darwin has been for SJG at the same time a crutch and a straw-man: a crutch because very skillfully he stressed the contradictions, the ambiguities and the theoretical flexibilities of the English naturalist in order to set them against the hardenings of the later Modern Synthesis (playing the game of who is more Darwinian than Darwin); a straw-man because he underlined, sometimes compulsorily, the supposed mistakes of Darwin as a gradualist and progressionist, in opposition to the radical reformation he had in mind after the Punctuated Equilibria paper.

As a matter of fact, despite Darwin's wedge of progress and liberalist economy of nature (two preferred polemic and "political" targets of SJG), they were two authentic pluralists. The main debt of SJG to Darwin is the idea of natural history as a domain of "laws" (lawlike patterns, regularities) interlaced with the domain of chance (irreversibility): uniqueness of history and repeatability of nature's patterns. Here is the grandeur of Darwin's view of life, and the key to understanding the central concept of contingency in SJG (Gould 1989, 1991, 1993; Pievani 2009). It does not mean that evolution occurred merely "by chance", but through an entanglement of functional factors (produced by selective pressures), structural constraints, and historical contingent events: an interplay between random events and regularities (Gould 2002a). The massive contingency of history means that particular events, or apparently meaningless details, were able to shape irreversibly the course of natural phenomena. We could define contingency (36 popular dedicated essays, but a theme quite everywhere present both in books and in the 136 peer-reviewed papers devoted to evolutionary theory) as the more general philosophical consequence of SJG's pluralism (A + B + C).

In this ambitious proposal of SJG as a philosopher of history, in a dialectic position with the founder, we recognize that each domain of his pluralism shows points of continuity and points of rupture with the Darwinian tradition:

- points of continuity are: in A, the role of geographic isolation, the Neo-Darwinian forces acting during speciation, the different levels of analysis with micro-evolutionary gradualism compatible with punctuations at the paleontological scale; in B, standard natural selection acting on organisms as a central mechanism being part of a hierarchical multilevel process, selection between tribes and families tolerated by Darwin in special cases; in C, both standard adaptations and functional shifts already discussed by Darwin;

- breaking points are: in A, no all-powerful phyletic gradualism, no progressionism, biological concept of species, neo-catastrophism; in B, no extrapolationism from lower levels (theory of microevolution), top–down interactions, species selection; in C, no prevailing functionalism as in Darwin, spandrels.

The global sense of SJG's peculiar operation on the Darwinian tradition has been the construction of a "third-generation" Darwinism, which (1) contains the nucleus of Darwin's theory (common descent, tree thinking, variation, inheritance, selective processes), (2) enlarges it in a plurality of rhythms, levels and factors, (3) cleans it from unnecessary hardenings of the late "dogmatic" Modern Synthesis (phyletic gradualism, extrapolationism, adaptationism). Considering in addition the growing historical awareness of the original Darwin's pluralism (about the three lines above: rhythms, levels and factors), even underestimated by SJG, we can agree with the very clear and somehow surprising statement of Niles Eldredge 2013

> And, I must also say, in an evolutionary context, Steve was as much of an adaptationist as the next person. I know it sounds strange to say so, given his reputation as a critic of hyperadaptationism—and his search for alternative explanations for morphological change in evolution (as witness his enthusiasm for Elisabeth Vrba's concept of "exaptation"—published as Gould and Vrba 1982—though the initial idea had been developed by Vrba). All that is true—but at heart he was a neo-Darwinian always. As am I—and so are we all.

## 4 Hierarchies and Levels of Selection

But Niles Eldredge stresses also another synthetic point: "Steve, at heart, was first and always a morphologist and developmentalist" (Eldredge 2013). In other words, strongly focused on internal constraints, developmental processes, complex forms: an internalist view of evolution (the third domain of his pluralism, C in Table 1, maybe the most relevant). We have seen above that points of rupture and points of continuity (with respect to the Darwinian theory) are consistent with each other because of the different scaling of evolutionary causality, a crucial issue for SJG. Nevertheless, as Niles Eldredge points out in his contribution in this volume (2013), the novelty of Punctuated Equilibria was not only related to the rates of speciation (the axis of time in representing evolution), a matter given undue weight in debates, with confusion between Punctuated Equilibria and versions of "saltationism" (Dennett 1995). The novelty was mainly related to the ecological, biogeographical and macroevolutionary conditions surrounding speciation processes (the axis of space in representing evolution: Vrba and Eldredge 1984; Eldredge 1989), like climate instability, geophysical disruptions, ecological barriers, fragmentation of habitats, and their consequences (turnover pulses, habitat tracking, mass or regional extinctions). Then, not only the "tempo" but also and mostly the "mode" of evolution.

It is interesting that about the “mode” of evolution (ecology, geography, and so on) a difference of sensitivity emerged in early times between SJG and Eldredge. As an extension of Punctuated Equilibria, in SJG, genomes, organisms and groups (even species for some characters like the degree of internal genetic variability) are different, inherently hierarchical levels of evolving “Darwinian units”: autonomous and integrated levels of the organization of life. In Lloyd and Gould (1993), species selection on “variability” (intended as a good species-level trait associated with genuine species-level fitness) was depicted as a major force of macroevolution (see also Gould and Lloyd 1999).

The fact that SJG intended hierarchical levels merely as sets of Darwinian units is relevant. Defining the levels of selection as units of interaction, rather than units of inheritance (see also Minelli 2013), SJG showed his mainly antagonistic way to interpret the “multilevel selection” debate (which is related but theoretically non coincident with the problem of the evolution of the hierarchical structure of the living world). He had steadily in mind the intellectual fight against Richard Dawkins and his gene-centered reductionism, so he thought to simply broaden the concept of replication. The result is a hierarchy with standard organism-like units (groups, species, super-organisms), intended as interactors, with the risks related to a strongly discontinuous concept of macroevolution as independent theoretical domain. Differently, in Eldredge the “hierarchy approach” is a more externalist extension of the mode of speciation inherent in Punctuated Equilibria, with a double genealogical (time) and ecological (space) logic (Eldredge 1999). The two parallel hierarchies in Eldredge are not a prosecution of Dawkins’ replicator/interactor scheme, because they are two causally inter-dependent levels of evolutionary change. On the contrary, in Dawkins interactors are mere vehicles for replicators and the replicative logic is the fundamental one.

The refusal of the double hierarchy of his friend and colleague is based, in SJG (2002a, p. 642), on two misleading arguments: useless complexity and overlapping (see also Minelli 2013). In Eldredge’s “sloshing bucket” model (2008), the nested evolutionary individualities are defined as kinds of biological organization, from the point of view of genetic transmission (genealogical or evolutionary hierarchy) and from the point of view of exchanges of matter and energy (ecological or economical hierarchy). Thus the groups of organisms inside a species, at the same population level above organisms, could be organized in two different ways. It is not essential that replication is a necessary and sufficient criterion for individuality, because the two hierarchies are not independent, but interdependent. In Eldredge’s model no faithful inheritance is required and the levels are wider units of evolutionary change (ecological and genealogical). In this case SJG’s criticism is linked to a rigid way to see hierarchy in an exclusively selective way (*contra* Dawkins), trying to define what exactly should be an “individual” (where species become “individuals” as well).

Hence all the problems related to “species selection” (and to strong versions of “group selection”) arose as well. “Interactors with adequate modes of plurification” (Gould 2002a, p. 642) is a quite vague definition, with serious difficulties at higher levels of the hierarchy. Moreover, “selection” is a very demanding causal concept and it is not enough to have somehow a discrete individuality for representing a unit of selection: without species-traits, competition, differential survival and inheritance of some kind no natural selection occurs. In Eldredge's (2008) model, standard natural selection between organisms is the hinge of the scheme, the locus where ecological logic and genealogical logic melt and coincide at the organismal level. No other metaphysical and unsteady definitions of "emergent properties" are needed to see standard natural selection as causation everywhere compulsorily. Instead, considering a stronger continuity between levels, we could observe "multilevel selection" processes depending on the different interactions (ecological and genealogical) below or above organisms: for example, phenomena of species sorting; phenomena of group selection depending on social organization and population structure; changes of the units of evolutionary change; trade-offs between selective forces, random events and structural changes; interplays between biological and cultural evolution. This kind of pluralistic explanation fits very well with a lot of contemporary integrated field researches, in which molecular biology, paleontology, ecology, paleo-climatology, demography, population structures, and other points of views at different levels (ecological and genealogical) make evidences and patterns to converge in shaping an evolutionary scenario, for instance in palaeo-anthropology (Jacobs and Roberts 2009; Pievani 2012c).

In this case we have different confronting kinds of pluralism (selective hierarchy of interactors *vs* ecological-genealogical hierarchy), that could be surpassed by new evidence and even appear as oversimplifications in the future. More generally, not only about the units of selection debate, adopting a "parliamentary metaphor" we envisage three possible positions about the future of the Neo-Darwinian research programme:

(a) *Conservatives*. Extensions are sufficient and they are already incorporated in the Modern Synthesis (like neutralism and near-neutralism), so the programme needs just superficial restyling case by case.
(b) *Revolutionaries*. Extensions are insufficient and the programme is going to become regressive, because it accumulates more and more serious and fatal anomalies. A rival research programme, no longer Darwinian, will replace the present one.
(c) *Reformists*. Extensions are insufficient, but they could be incorporated in a revised research programme, still Darwinian in its core but re-established both experimentally and theoretically, or in multiple theories with specific mechanisms and *explananda*.

As a matter of fact, it seems that the consensus of the many involved in theoretical issues of evolutionary biology is concentrated at present in the third position (see also Müller 2013). SJG proposed a "new synthesis", a new version of Darwinism, as an expression of the reformist claims. He envisaged neither an alternative "paradigm" (despite his attraction for Thomas Kuhn's "punctuational" way to see the history of science, SJG used this term for his opponents, for example labeling the "adaptationist paradigm"), nor a rival research programme.

He tried to trace the lines for updating the existing one (Pievani 2012a) . Then it is inaccurate to say that SJG has been a "failed revolutionary" (Dennett 1995). As a reformist, he was radical in some points and quite moderate in others. Provident or not has he been in this enterprise, he understood that it is not enough to say that a research programme (the Modern Synthesis) is in the middle of a crisis (regressive), and that recent advances are deeply innovative. He proposed a frame for the future evolutionary research programme to be "progressive" (in Lakatos' terminology), and any proponent of "extended" new syntheses should acknowledge it.

## 5 Discussion: How Much Extended the "Synthesis"?

As main focus of his heritage, SJG was not a science communicator, but an evolutionary biologist skillfully using history and philosophy of science for an ambitious proposal of revision and extension of the structure of evolutionary theory. He was not an anti-Darwinian (i.e. saltationist) or a post-Darwinian. He was historically aware in his scientific challenges, defending the autonomy of paleontology, the role of natural sciences and the morphologist and developmentalist traditions of research.

SJG's pluralism (A + B + C) is an "adaptive radiation" of possible directions of change in contemporary evolutionary research programme. In other words, an agenda for future research. In these first ten years without SJG, his proposals and provocations suffered a differential survival. Probably SJG was partly wrong about the non-functional role of non-coding DNA, claiming for a vague role of "biological redundancy" and flexibility. His analysis of the Burgess Shale general dynamics has been questioned (Collins 2009). Species selection is very seldom considered in current literature. Even some historical interpretations in his anthropological essays have been criticized (Lewis et al. 2011; see also Tattersall 2013).

On the contrary, if we focus on the main topics of A + B + C, according to Pagel et al. (2006), Punctuated Equilibria are far from being "a tempest in a teapot", as Richard Dawkins imprudently asserted. Their relative frequency, as one of the patterns of speciation, is substantial (for a reconstruction of the debate: Sepkoski 2012). Group selection, whatever its frequency or rarity in natural history, seems a real pattern, empirically testable (Goodnight and Stevens 1997; Nowak 2006; Wilson 2012). From a theoretical point of view, we have by now in the literature several proposals of multilevel or hierarchical selection theories, even if each author has a different version (Okasha 2006). About the present uses of three crucial SJG's concepts—such as heterochrony, developmental constraints and constructional non adaptive byproducts—as powerful theoretical frameworks see Müller (2013). Exaptations received growing quotations as mechanisms of change, not only in strictly biological fields (Pievani 2003, 2011; Pievani and Serrelli 2011).

Discussions are open about the empirical importance and relative frequencies of these patterns, but around the basic issues of SJG's overall proposal a pluralistic consensus seems to be gaining ground (Lewontin 2008). The future will say if this extension of the theory is becoming too large and frayed, and requires a more fundamental reduction to few principles. A first account of these ten years of new researches after SJG's death gives apparently two preliminary results:

(1) The amount of new discoveries with relevant evolutionary consequences (gene regulatory evolution, plasticity, epigenetics, niche construction, evolvability, and so on) went much beyond SJG's pluralistic expectations, making the "conservative" attitudes more and more anachronistic.
(2) In front of "revolutionary" temptations (the dawn of a new theory of evolution is coming), the reformists split between those who think that we need a succession of extended "special theories" with delimited *explananda* and mechanisms (see Müller 2013) and those who think that we need a third-generation "general theory" of evolution still Neo-Darwinian (after the original Darwinian one and the Modern Synthesis, like the "pluralist Darwinism" outlined by SJG). The former has the problem to figure out the theoretical and methodological relationships between the extended "special theories" and the supposedly basic "general theory". The latter has the problem to explain how the tumultuous empirical updates could be incorporated in a still coherent and unitary structure able to cover all kinds of evolutionary phenomena.

According to the methodology of scientific research programmes (Lakatos 1978), the "general theory" could be represented as an extended core of the programme (still Neo-Darwinian and corroborated) and the "special theories" as provisional extensions of the protective belt, subject to falsification. What is inside the core and outside the core depends on the relative empirical frequencies of the explanatory patterns (for an example of a very high frequency pattern: genetic drift), according to the current scientific literature. The internal theoretical coherence (in the core) and the increase of explanatory effectiveness and predictive power (in the belt) are two criteria to judge the scientific programme as "progressive" or "regressive", also with respect to possible rival research programmes.

Despite his stressing on cultural biases in science, "empiricist myths" and theory-data complex relationships (143 essays), SJG was not a sociological relativist, and never abandoned his scientific rationalism and even objectivist realism (Gould 2002a, p. 969). Thus, about the future of the structure of evolutionary theory, we could imagine that he would suggest to search for further empirical evidence in order to receive new, often unpredictable, answers from nature. In a Gouldian view: let us give the final word to the history of science, through a passionate and hopefully fair contest between pluralists and non pluralists.

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# Part II
# Genome and Development

# Molecules and Macroevolution: A Gouldian View of the Genome

**T. Ryan Gregory**

**Abstract** Stephen Jay Gould was a paleontologist by training, but his writing covered a wide range of topics and his thinking exerted an influence on several fields. Although he only discussed genome evolution only occasionally, it is clear that several "Gouldian" principles apply equally to this topic. These connections are explored in this review by using the evolution of genome size diversity—the so-called "C-value enigma"—as a case study. In particular, the hierarchical conception of macroevolution espoused by Gould is brought to bear on phenomena including the evolution of transposable elements within genomes and the effects of total genome size on higher level properties including at the cellular, organismal, and ecological scales. Conversely, some implications of an improved understanding of genome evolution for macroevolutionary theory are considered.

## 1 Introduction: Lessons from Prof. Gould

It is a testament to Stephen Jay Gould's enduring influence that a meeting celebrating his legacy can include so many disparate topics, ranging from paleontology to philosophy, from the history of science to developmental biology, and from anthropology to genomics. In part, this is because of Gould's unique ability to draw connections between seemingly unrelated topics and to synthesize information from a diversity of scientific disciplines. Indeed, he wrote on all of these topics to varying degrees during his prolific career.

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The breadth of Gould's influence also stems from the fact that he provided several important lessons that are applicable well outside of his own area of specialization. As notable examples, Gould's work frequently emphasized the importance of the following themes:

1. *Narrative*: It is important to understand the specific series of changes that have occurred over time, be it in an evolutionary lineage, a human institution, or even an individual lifetime. In other words, the details of "pure history" are relevant.
2. *Origins*: Not all aspects of complex biological systems are functional or adaptive. Many aspects of such systems evolve as byproducts of other changes ("spandrels"; Gould and Lewontin 1979) or first evolve for a function that is quite different from any role they may now serve. Thus, an examination of a trait in its current state or an assessment of its current utility (if any) does not provide an adequate view of how or why the trait originated in the first place.
3. *Exaptation*: Regardless of why they originated, be it adaptively or non-adaptively, features can become co-opted to serve new functions—that is to say, "exaptation" is a common process in evolution (Gould and Vrba 1982).
4. *Development*: It is not enough to consider either genes or phenotypic traits in isolation. Instead, we require an understanding of how they are connected through the process of development. Changes to the rate, proportions, quantity, or timing of developmental steps can be very important in shaping phenotypes (Gould 1977).
5. *Pluralism*: Small genetic changes accumulating slowly over time due to natural selection is not all there is—genetic changes may be large in effect, rates of change may vary dramatically over time, and non-adaptive processes may dominate in many cases (Gould 1980).
6. *Contingency*: Unique events can exert a large influence in the long run, even if they seem to be of only minor significance initially.
7. *Hierarchy*: Macroevolutionary questions often require complex answers that incorporate processes occurring at multiple scales, from within genomes to among species (Gould 2002).
8. *Scholarship*: It is important to know the history of one's field, lest one repeat the missteps of the past or neglect to recognize priority of discovery.

Although Gould's primary focus tended to be on paleontology and organismal biology, I have found each of these lessons to be highly applicable in my own research on evolution at the level of the genome.

## 2 Genome Size Diversity: A Classic Macroevolutionary Puzzle

Mass is one of the most straightforward properties of any physical entity, usually being much simpler than, say, structure or composition. It should therefore come as no surprise that the measurement of genome size (i.e., total mass of DNA[1]) began before the structure of DNA had been established and the major components of genomes identified. The first genome size estimates were performed in the late 1940s, at which time there was found to be "a remarkable constancy in the nuclear DNA content of all the cells in all the individuals within a given animal species" (Vendrely and Vendrely 1948; my translation). This observation of a constant and species-specific DNA amount was taken as evidence that DNA, and not protein, served as the hereditary material. It also led to the term "C-value" to describe the haploid nuclear DNA content (Swift 1950), a term still in wide use.

A few years later, Mirsky and Ris (1951) surveyed a taxonomically broad sample of animals and noted that DNA content and organismal complexity (taken as a proxy for the number of genes) were clearly unrelated. This finding has been overwhelmingly corroborated by the measurement of genome size for more than 10,000 species in the ensuing decades (Gregory et al. 2007), but it was a source of significant concern for many early geneticists. How could it be, they lamented, that lesser organisms like the "lowly liverwort" or a "slimy, dull salamander" have so much more DNA than humans (Comings 1972)? Bruised egos aside, there was also the important question of how it was possible for DNA amount, which is constant because it is the stuff of genes, to be unrelated to gene number. This perplexing contradiction became known as the "C-value paradox" (Thomas 1971). In like fashion, the more recently noted lack of association between organismal complexity and gene number itself has been dubbed the "G-value paradox" or "N-value paradox" (Claverie 2001; Betrán and Long 2002; Hahn and Wray 2002). As Harrison et al. (2002) asked, presumably with tongue at least partly in cheek, "How can our own supremely sophisticated species be governed by just 50–100 % more genes than the nematode worm?".

In all likelihood, the solution to the G-value paradox lies in differences in the regulation, expression, and interaction of genes, and in their capability in some cases to code for more than one protein product. This is, however, an avenue of post-genomic era research that is only just opening up, meaning that few conclusive answers are yet available. The C-value paradox, by contrast, was solved decades ago with the discovery that not all (or indeed, much) eukaryotic DNA consists of genes. In the human genome, for example, only about 1.5 % of the sequence is composed of protein-coding genes, and even if "genes" are defined

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[1] Genome size has traditionally been given in mass units of picograms (1 pg = $10^{-12}$ g), but is now also often expressed as total number of nucleotide base pairs (bp). The conversion between them is as follows: Number of base pairs = Mass in pg × 0.978 × $10^9$ and conversely, Mass in pg = Number of base pairs × 1.022 × $10^{-9}$ (Dolezel et al. 2003).

loosely to include the non-coding intronic portions, this still accounts for less than 30 % (International Human Genome Sequencing Consortium 2001). As noted, at about 3.5 pg the human genome is unremarkable in size relative to lowly liverworts, slimy salamanders, and many other groups whose proportion of non-coding DNA is much higher.

The presence of so much non-coding DNA dissolved the C-value paradox, but it also precipitated a new "C-value enigma" (Gregory 2001a), which includes both proximate and ultimate components: Where does this non-coding DNA come from? How can it be gained or lost from genomes? Does it have any impacts on the organismal phenotype? Is any of it functional? Why do some groups have a great deal of it, while others have relatively little? Clearly, the enigma of genome size diversity cannot be solved by any single approach (although this has certainly not stopped theorists from trying to do so). Because it deals with variability among species and higher taxa, the evolution of genome size is, by definition, a macroevolutionary question. And macroevolution, as Gould argued, cannot be accounted for by processes operating at only one biological level. As described below, at least four levels of analysis must be invoked for an understanding of genome size evolution.

## 3 Level One: Processes Within the Genome

### *3.1 An Introduction to Transposable Elements*

Whereas less than 2 % of the human genome consists of genes, as much as two-thirds of it is made up of transposable elements (TEs) and their defunct remnants (de Koning et al. 2011). This represents the largest single contribution to genome size of any sequence type. Put directly, the story of genome evolution is, in an important sense, much more about TEs than protein-coding genes. It would therefore seem worthwhile to provide a brief overview of TE biology before moving on to discuss their contributions to genome size and evolutionary theory.

Transposable elements, it may be recalled, were discovered in the late 1940s by Barbara McClintock (whose findings eventually garnered her a Nobel Prize). As their name implies, TEs are mobile DNA sequences capable of autonomous movement and duplication within (and sometimes among) genomes. TEs are placed into two different classes, depending on their mechanism of transposition.

Class I elements ("retrotransposons") make use of an RNA intermediate when transposing, and are divided into three main types: (1) long terminal repeat (LTR) retrotransposons and endogenous retroviruses (ERVs), (2) non-LTR retrotransposons, also known as long interspersed elements (LINEs), and (3) short interspersed elements (SINEs). ERVs constitute about 8 % of the human genome, whereas LINEs and SINEs (collectively known as "retroposons") make up roughly 20 and 13 %, respectively (International Human Genome Sequencing

Consortium 2001). The *LINE*-1 element is present in the human genome in more than 500,000 copies, while the *Alu* element (a SINE) is found in over 1,000,000 copies (International Human Genome Sequencing Consortium 2001). As Doolittle (1997) put it, "Our genomes… contain 500,000 to one million copies of a short sequence called 'Alu'. Since we probably have [~20,000] 'real' (protein-coding) functioning genes, our genomes… might be ironically viewed as vehicles for the replication of Alu sequences". SINEs, unlike LINEs, do not encode the enzymes necessary for their own replication, and appear to be dependent on LINEs for getting around (e.g., Okada et al. 1997; Smit 1999; Weiner 2000). It has therefore been suggested that "SINEs are wildly successful freeloaders on the backs of LINE elements" (International Human Genome Sequencing Consortium 2001).

Class II elements are represented by the DNA transposons, which do not use an RNA intermediate, but instead propagate by the direct transposition from DNA to DNA by a "cut-and-paste" mechanism. This mode of transposition is not inherently duplicative and, as a result, these elements are comparatively rare in many animal genomes; they make up slightly less than 3 % of the human genome sequence, for example. DNA transposons rely in part on horizontal transmission (i.e., transfer to non-relatives, including across species boundaries) for their long-term survival, unlike the long-lived retroposons which rely almost exclusively on vertical transmission (i.e., from parent to offspring only), or the LTR retrotransposons which make use of both strategies (Burke et al. 1998; Malik et al. 1999; International Human Genome Sequencing Consortium 2001).

## 3.2 *"Selfish DNA" and Selection Within the Genome*

The notion that certain autonomous genetic elements might best be characterized as "parasites" of the "host" genome dates back at least to Gunnar Östergren's discussion of non-coding "B chromosomes" in plants in 1945.[2] As he put it, "I think reasonable support may be given to the view that in many cases these chromosomes have no useful function at all to the species carrying them, but that they often lead an exclusively parasitic existence". In order to persist, Östergren (1945) noted, "they need only be 'useful' to themselves", with the interesting implication that "a similar antagonism in the evolutionary tendencies as that between a parasite and its host should be expected between parasitic fragment chromosomes and the plants carrying them."

The application of such concepts to sequences located within the primary chromosome set (e.g., transposable elements) came more than three decades later, with brief discussions by Dawkins (1976) and Cavalier-Smith (1977), followed by an explicit development of the "selfish DNA theory" by Orgel and Crick (1980) and Doolittle and Sapienza (1980). This theory suggested that a substantial

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[2] See Camacho (2005) for a detailed review of B chromosome biology and evolution.

fraction, perhaps even a large majority, of eukaryotic DNA persists by virtue of its own capacity for self-propagation, independent of any functional significance for organisms. In fact, the accumulation of such "selfish DNA" was taken to be mitigated only when its replication became too costly for the host organism.

This notion of "selfish DNA" was met with some resistance in the early stages (see Doolittle 1981, 1982). Even Gould (1983, p. 173) objected to the concept, arguing that "selfish DNA is about the worst possible name for the phenomenon, for it records the very prejudice that the new structure should be combating: an exclusive focus on [organisms] as evolutionary agents. When we call repetitive DNA 'selfish', we imply that it is acting for itself when it should be doing something else, namely, helping [organisms] in their evolutionary struggle."[3] However, since the prevailing view of genomic DNA *was* that it should have a ubiquitous organism-level function—the view that the concept of selfish DNA sought explicitly to challenge—this seems a rather strange criticism. Notably, Doolittle and Sapienza (1980) included a favourable citation of Gould and Lewontin's (1979) famous "spandrels" paper in the opening section of their article. Moreover, the "selfishness" of transposable elements need not refer to the level of the organism at all, but rather to that of the *genome*, where replicational cooperation with genes and other elements might reasonably have been expected.

## *3.3 Parasites, and More*

Parasitism is only one way for symbionts to interact with their hosts, and in many cases there can be significant pressures to evolve reduced virulence. Since the fate of most TEs is ultimately linked to the survival of their genomic hosts, there may be a tendency toward the evolution of "selfish DNAs with self-restraint" (Doolittle et al. 1984). The modern view of TEs takes an even broader view, with these elements seen as operating along the entire ecological continuum from parasitism to mutualism (Kidwell and Lisch 2000, 2001). For example, while some TEs can cause potentially serious mutations (including some linked to cancer and other diseases; e.g., Chen et al. 2006; Schulz 2006; Babushok and Kazazian 2007; Belancio et al. 2008), others may insert preferentially into non-coding regions so as to remain mostly benign (or commensalistic, to stick with the ecological terminology; e.g., Dimitri and Junakovic 1999; Hutchison et al. 1999). Examples of mutualism, in which TEs have taken on regulatory or other generalized functions in the genome, are also becoming increasingly common (e.g., Brosius 1999;

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[3] Although Gould appreciated the important theoretical implications of selfish DNA (as discussed in a later section), he maintained this critical view of the terminology right through to his last contribution on the subject: "Such genes could only be deemed 'selfish', 'parasitic', etc., from a false and limited perspective that values the organism alone as an agent of evolutionary success. After all, we don't call a peacock selfish for evolving such a beautiful tail, and thus limiting the geological longevity of the species" (Gould 2002, p. 694).

Kidwell and Lisch 2001). It has been estimated that as much as 25 % of human regulatory regions are derived from former transposable elements (Jordan et al. 2003). Gould was aware of the potential of TEs to be co-opted into functional roles at the organism level, having used this as an example in the original "Exaptation" paper (Gould and Vrba 1982) and even going so far as to propose a new terminology for non-coding DNA to reflect this potentiality (Brosius and Gould 1992).

While certainly more expansive than the purely parasitic view of TEs, this brief discussion is still somewhat superficial. Transposable element biology can (and should) often be viewed in ecological terms, with TEs living and interacting within a diverse genomic ecosystem. This can involve competition for preferred insertion sites ("territory") or replicational materials ("resources") between variants of the same element type ("conspecifics") or unrelated ones. Some TEs may be reliant on others for their survival, as with the dependency of SINEs on LINEs for propagation. The list of ecological parallels could go on, and shows that there is much more to evolution within the genome than simple antagonism between TEs and their hosts (Linquist et al. 2013). Of course, this is only one level of interest among several.

## 4 Level Two: Effects on the Cell

### *4.1 The Ubiquitous Correlation*

It has been recognized for well over a century that nucleus size and cell size are strongly positively correlated (e.g., Gulliver 1875). For more than 60 years, this has also been known to extend to correlations with genome size itself (e.g., Mirsky and Ris 1951). The correlation is found in both animals and plants, and has been particularly well demonstrated using vertebrate red blood cells (see Gregory 2001a, b, 2005a, b, c, d for reviews). In fact, this positive relationship with cell size is what Cavalier-Smith (1982) called "the most reliably established fact about genome evolution". The rate of cell division, on the other hand, is negatively correlated with genome size, meaning that a large genome is associated with large, slowly dividing cells.

In mechanistic terms, a link between genome size and cell size may arise via the intermediate of cell division rate. Specifically, because cellular growth occurs throughout the cell cycle, any delay in division will result in the production of larger daughter cells. Not only does more DNA take longer to replicate (i.e., prolong the synthesis phase, or S-phase), but larger nuclei may also delay the accumulation of molecules (cyclins) that trigger the progression from one phase to the next (most notably, from the first gap, or $G_1$-phase, to S-phase) (see Gregory 2001a for a detailed discussion of the model). This approach has the advantage that it accounts for both the cell size and division rate correlations, and is also able to explain some otherwise puzzling observations. For example, red blood cell size and genome size are positively correlated in mammals, even though mature mammalian erythrocytes do not contain nuclei (Gregory et al. 2000). If DNA content influences the division of the progenitor cells (which do contain nuclei), then this effect would be carried over to the enucleated red blood cells.

## 5 Level Three: Impacts on the Organismal Phenotype

Whatever its mechanistic basis, a causative link between genome size and cellular parameters means that bulk DNA amount, much of it consisting of transposable elements, can clearly exert important effects at higher levels of biological organization. This is not restricted to the cell level, because cell size and division rate may in turn impact upon key organism-level features. Most obviously, if the number of cells is not adjusted accordingly, then a change in individual cell size will necessarily induce a change in body size; ion and gas exchange rates are greatly affected by shifts in cell surface area to volume ratios (which decrease with increasing cell size), such that larger cells may be associated with lower metabolic rates; slower cell division could obviously influence the overall rate of development; and so on. While numerous examples of such relationships exist, it is apparent that the genome size-cell division-cell size correlations play out in different ways at the organism level, depending on the biology of the group in question.

### *5.1 Body Size*

In mammals, variation in body size is largely a product of differences in cell number, and so is not generally correlated with cell or genome size (Gregory 2002a). Where correlations with body size are particularly evident is in small-bodied invertebrates such as flatworms, copepod crustaceans, and certain insects (e.g., Gregory et al. 2000).

### *5.2 Metabolism*

A high metabolic rate (measured as the rate of oxygen consumption per unit mass) requires efficient gas exchange, which is aided by having high cellular surface area to volume ratios, which in effect means having small cells. Because cell size IndexTerm>Cell size is influenced by DNA content, it has long been argued that genome size should be associated with metabolic rate in vertebrates (e.g., Szarski 1970, 1983; Cavalier-Smith 1978). To be sure, the hot-blooded homeotherms (i.e., mammals and birds) generally have much smaller genomes than the more lethargic amphibians and lungfishes (Gregory 2001c). However, overall a relationship with metabolic rate cannot account for all genome size diversity, given that the smallest vertebrate genomes are found in teleost fishes, and that reptiles have smaller genomes on average than mammals (this latter point probably relates to the enucleation of mammalian erythrocytes, which allows them to achieve much smaller cell sizes despite having somewhat larger genomes; Cavalier-Smith 1978). Moreover, while metabolic rate does correlate negatively with genome size in both mammals and birds (Vinogradov 1995; Gregory 2002b), such a relationship is not found within the amphibians despite their 120-fold range in genome size (other than the difference between frogs, which are relatively motile and have smaller genomes, and salamanders, which are more sessile and have large genomes; Gregory 2003).

## *5.3 Development*

In direct contrast to the situation with metabolic rate, amphibians show a clear association between genome size and developmental rate, whereas mammals and birds display no such correlation (Gregory 2002a, c). A negative correlation has also been shown in various arthropods (McLaren et al. 1988; White and McLaren 2000; Gregory and Johnston 2008). In plants, the clearest relationship is not with developmental rate *per se*, but rather with developmental lifestyle. Thus, annuals (species that complete their life cycle within one year) have smaller genomes than perennials (which take more than one year) (see Bennett and Leitch 2005 for review).

It is important to note that *rate* (how quickly it occurs) is only one side of the developmental coin; the flip-side of this is *complexity* (how much change must be accomplished). In this sense, rate is only relevant as a correlate of genome size when complexity is held essentially constant—that is, if all the species being compared have roughly the same amount of developing to do. Conversely, if the time available for development is held constant, then the relevant consideration will be how much morphological change must be carried out in that limited time period. The clearest example of this comes from amphibians, in which there is an obvious time-limited period of intensive morphological differentiation, namely metamorphosis. Thus, the smallest amphibian genomes are found in frogs that inhabit short-lived pools and which must therefore complete their development rapidly before burrowing underground to survive the lengthy dry season. Direct-developing frogs, which undergo their development within the egg and hatch as tiny "froglets", are next on the genome size scale, followed by normally metamorphosing ("biphasic") frogs (Gregory 2002c).

There is no overlap between frog and salamander genome sizes, which itself could reflect the much simpler metamorphosis of the latter. Within salamanders, biphasic species have the smallest genomes, followed by direct-developers and those that metamorphose only occasionally ("facultative neotenes"), those that normally do not metamorphose but can be stimulated to do so by hormone (thyroxin) treatment ("inducible neotenes"), and finally those that can never metamorphose under any conditions ("obligate neotenes"). By all indications, obligate neoteny has evolved independently at least three times in the Amphibia, each time associated with the possession of an exorbitant genome (Gregory 2002c). Importantly, fossil cell size data clearly indicate that extraordinary genome sizes of both salamanders and lungfishes are derived features, having evolved along with or after changes in the developmental program (Thomson 1972; Thomson and Muraszko 1978). A similar process appears to be in operation among insects, with those orders displaying complete metamorphosis (holometabolous development) having genome sizes under 2 pg and those with no (ametabolous) or incomplete (hemimetabolous) metamorphosis exceeding this threshold by a wide margin in many cases (Gregory 2005a, b, c, d).

### *5.4 Other Features*

The combination of larger cell size and slower cell division can make for some very interesting effects of large genome size. In the extreme case where cell number is held constant ("determinate growth"), this can result in impacts on both body size and developmental rate, as with some copepod crustaceans (McLaren et al. 1988). In some vertebrates, it is just the opposite problem: the sizes of some organs cannot increase along with cell size, meaning that cell numbers must be reduced. This is particularly relevant in miniaturized animals, such as in salamanders of the tribe Bolitoglossini (family Plethodontidae) which have both tiny bodies and large genomes (they are direct-developers). A small body means a small brain case, but a large genome means large and slowly differentiating neurons and thus a greatly simplified brain (Roth et al. 1988, 1990, 1994, 1997). Of course, salamanders are not known for their intellectual prowess in any case, but here the result has been especially pronounced, with the visual processing centers compromised in such a way as to make their former lifestyles as active predators impossible (Roth et al. 1988, 1990, 1997).

## 6 Level Four: Ecological and Evolutionary Constraints

### *6.1 Top-Down Constraints*

As expected under standard Darwinian theory, pressures derived from external ecological conditions will affect the evolution of the features described previously, and therefore indirectly constrain the evolution of genome size. For example, metabolic rate is an especially important consideration for organisms engaged in powered flight, and it is notable in this regard that the only truly volant vertebrates, birds and bats, have conspicuously small genome sizes among the tetrapods (Andrews et al. 2009; Smith and Gregory 2009). Some molecular mechanisms have already been identified that act to keep genomes small in these groups (Baker et al. 1992; Van Den Bussche et al. 1995). In fact, there is even a significant association between measures of flight ability and genome size within the birds (Andrews et al. 2009), with the largest genomes found in flightless groups (Hughes 1999; Gregory 2005a, b, c, d) and the smallest in hummingbirds (Gregory et al. 2009).

The case of amphibian development is also informative in this context. It may be, for example, that the tightly constrained genome sizes of certain frogs are indirect adaptations (via selection for rapid developmental rate and thus for fast cell division) to life in short-lived water bodies. Conversely, the relaxation of ecological constraints may allow an increase in genome size. This is illustrated by the association between the loss of metamorphosis and the growth of the genome in neotenic salamanders. In general, metamorphosis from aquatic larva to terrestrial adult is favoured when conditions in the water are poor (e.g., low food availability, high predation, low oxygen). Metamorphosis may be eschewed when conditions are favourable, however, and the longer this persists, the more likely it will be that a mutation in a crucial gene will make metamorphosis difficult or impossible (Gould 1977). A persistent avoidance of metamorphosis will not only allow such genes to mutate freely, it will also remove the constraint on genome size imposed by the need for rapid tissue differentiation, and thereby permit the accumulation of non-coding DNA (Gregory 2002c).

## *6.2 Bottom-Up Effects*

While there is good reason to accept that ecological constraints can have downward effects on the evolution of the genome, it may be unwise to view causation as strictly unidirectional. Thus, it is also possible that small genomes are “preadaptations” for flight, the invasion of temporary ponds, or holometabolous development (Gregory 2002b, c). Certainly, there is evidence that genome size reduction had begun in theropod dinosaurs prior to the evolution of flight (Organ et al. 2007). Similarly, the accumulation of DNA could itself hinder the process of metamorphosis, and help to make neoteny obligate in certain salamander lineages (Gregory 2002c). Of course, all of these cases could involve a bidirectional feedback, so these are not necessarily alternative interpretations.

Clearer illustrations of a bottom-up influence of genome size on ecology can also be found. In plants, for example, large genomes appear to be associated with heightened tolerance to drought (e.g., Castro-Jimenez et al. 1989; Wakamiya et al. 1996) and frost (e.g., MacGillivray and Grime 1995). Thus, certain environmental conditions may favour plants with larger genomes. On the other hand, there is growing evidence that large-genomed plants are excluded from extreme environments (Knight et al. 2005) and are more susceptible to pollution (Temsch et al. 2010). All of these findings suggest that genome size may play a role in shaping the distribution of species observed at large geographic and ecological scales, especially in light of the increasingly severe effects of human activity on the environment.

Perhaps the most interesting example of a bottom-up constraint is provided by the miniaturized salamanders described above. To reiterate, the combination of a reduction in body size and a large genome size has generated simplified brains consisting of few, large, slowly-dividing neurons. A neurologically demanding visual predation strategy is no longer possible under these conditions, with the net result being a shift to a lie-in-wait strategy and the associated evolution of a highly specialized projectile tongue (Roth et al. 1990, 1997). In this case, an increase in genome size, together with a major morphological shift towards smaller body size, has substantially altered the ecological lifestyle of a prominent lineage.

## 7 Genome Evolution from a Hierarchical Perspective

### *7.1 Selfish DNA and Its Hierarchical Implications*

Whatever one's feelings about the term "selfish", the important point is that the existence of parasitic DNA elements implies the operation of natural selection on at least one level in addition to the standard organism level. Specifically, the spread of parasitic forms of non-coding DNA can be seen as proceeding by a process of "intragenomic selection" (Cavalier-Smith 1980). This has been recognized since the earliest days of the parasitic DNA approach; as Östergren (1945) himself noted, "the units of selection" in such cases are "not the biological individuals but their genes and chromosomes". Selection within the genome, as well as on the organism, would therefore be necessary in order to account for even the most basic aspects of genome organization (Sapienza and Doolittle 1981; Doolittle 1989; Gregory 2004a, b).

Thus, even in its very simplest formulation, the selfish DNA theory has obvious implications for a hierarchical approach to macroevolution. Again, this fact was well appreciated by Gould (1992), who admitted that "punctuated equilibrium is but one pathway to the elaboration of hierarchy, and probably not the best or most persuasive; that role will probably fall to our new understanding of the genome and the need for [intragenomic] selection embodied in such ideas as 'selfish DNA'." A few years earlier, Doolittle (1989) had published an explicit discussion of the two-level hierarchical implications of selfish DNA, but for the most part there has been very little cross-talk between genome biologists and paleontologists, despite this obvious area of common interest.

## *7.2 A Gouldian View of the C-Value Enigma*

As Gould (1995) noted, “In the world of hierarchical selection, stable systems usually represent balances of negative feedback between adjacent levels.” C-values are examples of stable systems *par excellence*, and there is much reason to believe that the genome size of a species is partly the result of a balance among different levels of selection. Intragenomic selection among transposable elements may exert a bottom-up pressure toward genomic growth, but the spread of subgenomic elements can be constrained by selection on genome size operating at the organismal level (e.g., metabolic rate, developmental rate). Importantly, the specific constraints on genome size vary according to the biology of the organisms in question (e.g., endotherms vs. amphibians). In some groups, constraints on subgenomic elements (like TEs) may be released due to a change in organismal biology (e.g., loss of flight in birds, neoteny in amphibians). An important consequence of this view is that genome size itself may be under selection (at multiple levels), but a given C-value may or may not be “adaptive” in any particular case.

## *7.3 An Expanded Hierarchical View*

Following Gould (1992), we can see that the study of transposable elements provides one of the clearest demonstrations of hierarchical selection in action, meaning that it ought to be of considerable interest to macroevolutionary theorists. However, true integration between disciplines should proceed in both directions, and it is therefore worthwhile to ask how concepts derived from paleontological theory might inform the study of the genome.

An important component of macroevolutionary theory is the distinction between sorting (a pattern of differential survival and reproduction) and selection (one possible cause of sorting). Standard neo-Darwinian theory is based almost exclusively on the organism level, where there is no controversy regarding the efficacy of selection and other processes (e.g., genetic drift) for producing patterns of sorting. Selection at the species level, on the other hand, can be very difficult to demonstrate in practice, and in fact there is only limited agreement as to what would actually constitute legitimate species selection. For example, under Vrba’s (1989) “effect hypothesis”, true species selection can be attributed to a pattern of sorting only when it involves “emergent characters” at the species level which cannot be reduced to the sum properties of their constituent organisms. When only “aggregate characters” are involved, this could count only as a bottom-up effect on species-level sorting, not selection. Lloyd and Gould (1993), by contrast, argue that so long as the fitness consequences of an aggregate character are felt at the species level, then sorting based on “emergent fitness” would also count as selection. Finally, there can also be top-town influences, since the fitness of organisms is partly dependent on the species-specific context in which they live.

Vrba (1989) illustrates this notion of “context-dependent sorting” with the following analogy: “To the extent that a national ruler or law dictates that members of the population with certain characteristics may have more children than others, or must die at different ages, sorting among humans depends on whether they live in that nation or in another more liberal one”.

Again, these concepts—selection versus sorting, emergent vs. aggregate characters, the effect hypothesis versus emergent fitness, and context-dependent sorting—were all developed with the species level in mind. The question here is whether they apply as well (or perhaps even better) to questions of genome evolution. That they do is apparent when the preceding discussion of genome size evolution is recast in the following terms: (1) genome size is an *aggregate character*, representing the sum of all sequences contained within it, many (but not all) of which spread by intragenomic selection, (2) in this genome size aggregate, these sequences exert important *emergent fitness* effects on the cell, which in turn are felt at the level of the organism (e.g., body size, metabolism, development) and above (e.g., ecological parameters such as predation strategy), and (3) ecological and evolutionary constraints also operate in a top-down manner, with *context-dependence* playing a major role in determining the relative success of subgenomic elements; from the perspective of a transposable element, the genome of a bird would be considered a harsh totalitarian regime, whereas that of a neotenic salamander is extraordinarily tolerant.

As part of his classic hierarchical treatment of selfish DNA, Doolittle (1989) suggested that “it is not clear that we can so easily understand all of the structures and evolutionary behaviors of DNA without some further theoretical expansion.” Based on the above, it would seem that the theoretical expansion needed in this case is the same as that required at the highest scales of evolutionary analysis.

## *7.4 Genomes and Macroevolutionary Theory*

The development of the theory of punctuated equilibria in the early 1970s raised an important challenge to the assumptions of neo-Darwinian orthodoxy, namely that the patterns observed at the highest evolutionary scales do not conform to the predictions of models based solely on gradual changes in allele frequencies within populations (Eldredge 1971; Eldredge and Gould 1972). It also lent substantial support to hierarchical selection theory by granting to species many of the traits necessary for qualification as Darwinian individuals (i.e., births, relatively stable lifespans, deaths, and the production of offspring). Not surprisingly, this fed directly into the long-standing (and still ongoing) debate surrounding the mechanistic continuity, or lack thereof, between micro- and macroevolution. What is perhaps less widely appreciated is that a great many expectations of the Modern Synthesis regarding the workings of heredity—that is, the lowest evolutionary scales—have likewise been challenged by new knowledge about genes and genomes. In this context, we should not forget that both Darwinian natural selection and neo-Darwinian population genetics were developed long in advance of modern genomic analysis, and indeed prior to the elucidation of the structure of DNA or even its identification as the hereditary material.

Consider the following dozen discoveries in genetics and comparative genomics made *after* the construction of the Modern Synthesis, none of which was anticipated by the theory: (1) the existence of "transposable elements" capable of self-propagation within genomes, (2) the total disconnect between the amount of DNA in a given eukaryote genome and the complexity of the organism containing it, (3) the disconnect between number of protein-coding genes and organismal complexity, (4) the key evolutionary role played by duplications of individual genes, large sections of chromosomes, and entire genomes, (5) a great preponderance of non-adaptive, "neutral" evolution at the molecular level, (6) the existence of highly conserved developmental regulatory genes across distantly related taxa, (7) the staggeringly low gene numbers in the genomes of even the most complex organisms, (8) the capacity of single coding genes to generate numerous protein products by "alternative splicing" thanks to the presence of non-coding introns, (9) the co-option of formerly parasitic genetic elements into regulatory functions by the host genome, (10) the horizontal transfer of genetic material among species, perhaps even across kingdoms, (11) the lack of monophyly in numerous classically recognized taxa such as "reptiles" and "fishes", and most notably the fundamental divide between the Archaea and Bacteria, and (12) the pronounced genic similarity between some morphologically divergent species (e.g., humans and chimpanzees) contrasted against the extensive molecular divergence found among many otherwise cryptic species.

"That advances in molecular biology contribute to the need for a formal expansion of evolutionary theory," Eldredge (1985, p. 86) noted almost three decades ago, "is an exigency we can hardly hold against the early architects of the synthesis". On one level, this will involve an expansion of microevolutionary theory to accommodate novel mutational mechanisms and a new understanding of how genotypes result in phenotypes. More broadly, it must also include an explicit recognition that macroevolutionary questions must be treated at levels in addition to populations of organisms. Take, for example, the afore-mentioned discovery that development is greatly influenced by a relatively small set of clustered regulatory genes. At levels below the organism, genome biologists may inquire as to what role gen(om)e duplications have played in shaping these gene clusters, how broadly conserved they are among taxa, and how their structure is linked to changes in developmental complexity (e.g., Holland et al. 1994; Sharman and Holland 1996; Martin 1999; Ferrier and Holland 2001; Larhammer et al. 2002; McLysaght et al. 2002; Ronshaugen et al. 2002). Population geneticists, for their part, may fairly ask how such genes would have been filtered by the microevolutionary processes of selection and drift within populations in order to reach an evolutionarily relevant frequency (e.g., Johnson and Porter 2001). Macroevolutionists, meanwhile, may be interested in the importance of such genes for the emergence of new body plans and other evolutionary novelties with cascading macroevolutionary consequences (e.g., Carroll 2000; Erwin 2000; Jablonski 2000;

Shubin and Marshall 2000). Without question, a complete understanding of this topic would necessarily involve inputs from all three evolutionary scales (as well as from studies of gene transcription, cell signaling, and developmental biology).

Macroevolutionary questions, from the evolution of genome size to patterns of diversification in deep time, cannot be fully understood only with reference to the population level, and thus must be discussed from a perspective outside standard neo-Darwinian theory. Genome size, in particular, clearly involves bidirectional interactions among several levels of organization, both above and below organisms within populations. However, it does not follow from this that microevolutionary theory is of little relevance to such issues. For one thing, some of the component questions of the C-value enigma are explicitly microevolutionary in nature, as with the mechanistic issue of how genomes change in size. The smaller-scale evolution of transposable elements has been well studied from a microevolutionary perspective, and even large-scale changes in genome size (e.g., by wholescale duplication) must somehow go from rare novelty to observable commonality. Explaining how this occurs is the domain of an expanded microevolutionary theory in which any genetic variant, including different genome sizes, can be considered as an "allele". The important issue is to identify all of the factors that contribute to the success or failure of genomic variants, for which reference must be made to other levels in addition to individual organisms. As Gould (1982) put it, "nothing about microevolutionary population genetics, or any other aspect of microevolutionary theory, is wrong or inadequate at its level… but it is not everything".

From the point of view of genome size evolution, microevolution and macroevolution are neither conflicting alternatives nor different views of the same thing. Rather, each deals with a different set of questions and both are necessary for a complete understanding of the complex puzzle at hand. While genome size evolution provides one of the clearest cases in which this is true, it is not the only one. In order to be properly understood, any macroevolutionary question must be considered from various perspectives, including mutational processes within the genome, mechanisms of developmental regulation, the genetics of populations, the patterns of relatedness among groups, and the input of large-scale historical and ecological factors.

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# Individuals, Hierarchies and the Levels of Selection: A Chapter in Stephen J. Gould's Evolutionary Theory

**Alessandro Minelli**

**Abstract** Darwin's theory of natural selection was a theory about microevolution which implied (1) that individuals organisms can be unambiguously recognized, (2) that what identifies the level, or levels, of selection is interaction rather than inheritance, and (3) that levels of selection other than the individual organism are either nonexistent, or of little relevance. In *The Structure of Evolutionary Theory*, Gould explained why the units of selection must be identified, contra Dawkins, in the units of interaction rather than in the units of inheritance, and why the whole theory of selection (and evolution) can be developed by reference to a single hierarchy of levels, or units, of selection. If Gould and Eldredge's model of punctuated equilibria represents the actual, or prevailing mode of evolution, species boundaries become less arbitrary than in Darwin's own view, and species eventually emerge with an individuality that turns them into potential units of selection. Recent advances in fields as diverse as symbiosis, lateral gene transfer and the evolution of development suggest that to shoehorn biological systems into the levels of the so-called evolutionary hierarchy is an oversimplification. Even the concept of individual organism as a physically independent unit with its precise origin in time does not apply so easily and universally as generally accepted. Evolution, indeed, is not simply matter of change of 'individuals', at any and all levels of the gene-to-clade hierarchy, but also matter of change of the units (or levels) of selection and of the rules of change themselves.

In his final, comprehensive account of evolutionary theory, Gould (2002) characterized Darwin's model—articulated around the three notions of variation, inheritance and selection (Darwin 1859)—as a theory of microevolution, with three important although very seldom highlighted implications. First, that individual organisms can be unambiguously recognized. Second, that what identifies the level, or levels, of selection is interaction rather than inheritance. Third, that no

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level of selection other than the individual organism exists, or is of some relevance. Are we still happy with these three implications of Darwin's theory of evolution? Do we need to revise them, or to add new dimensions to the theory? In the following pages I will briefly discuss these problems in the light of Gould's detailed analysis.

## 1 Biological Individuals

Occasionally, we are confronted with biological objects that we cannot confidently classify as individual organisms. The ambiguity of these objects is well expressed by our contrasting linguistic usage, as we prefer to speak of conjoined twins (Siamese twins) whenever these weird creatures show up in the human species, whereas the anatomical equivalent in a nonhuman species is usually described as a two-headed calf or the like. To be sure, in the case of human beings we are not so ready to deny individuality even to grossly incomplete units. These are anyway "monsters" one can perhaps ignore when trying to understand and define biological individuality. More serious problems are presented by the frequent cases where full anatomical independence (arguably, the prime criterion of individuality) is not accompanied by genetic uniqueness. This is a very common state of affair among plants, where physically separated organisms produced by vegetative reproduction are identical at the genetic level: to use Harper's (1977) terminology, those plants are distinct ramets of the same genet.

Comparable occurrences are less common among animals, but examples are known even in vertebrates, our own species included. This happens, indeed, in the case of polyembryony, that is, when two or more physically separated embryos develop out of a single fertilized egg. These identical twins are not so common in *Homo sapiens*, but are the rule in other species, for example in the nine-banded armadillo, where females give regularly birth to sets of four identical twins. Other organisms where the concept of individual does not apply in a clear, undisputable way are colonial animals such as corals. Here the single flower-like polyps are possible candidates to the status of biological individuals, despite their anatomical interconnections. Alternatively, however, we could recognize as individual the whole which could otherwise be called a colony—an individual, indeed, because of its anatomical and functional integration. As a third and possibly best option, anyway, when dealing with colonial animals be could consider abandoning altogether the use to the category 'individual'.

In the case of vertebrates, at least, a potential criterion of individuality is offered by the immunological specificity so obviously manifested in the case of organ transplants (see, e.g., Pradeu 2010). However, in this respect too there are exceptions that undermine the universality of an apparently sound criterion of individuality. In some abyssal fishes belonging to the Ceratioidea, close relatives of the angler fish, on finding a conspecific female the dwarf male attaches to her and the two partners eventually fuse together, even developing vascular interconnections, thus demonstrating their full immunocompatibility.

A major difficulty in discussing about the nature of biological individuals and their place in evolution is due to the lack of reliable and generally agreed definitions. Gould was perfectly aware of this problem, and remarked that "most authors use "organism" for the Darwinian body (me and thee) and "individual" for the generalized unit of selection at any hierarchical level, while others (like Wilson and Sober) imply reversed definitions" (Gould 2002, p. 601).

Traditional criteria of individuality such as physiological unity, genetic homogeneity, and genetic uniqueness do not offer a universal solution (Folse and Roughgarden 2010; Pradeu 2010) and a pluralistic approach to the problem of biological individuality has been repeatedly defended (e.g., Santelices 1999; Wilson 1999; Dupré 2010). A largely applicable "generative" foundation of the concept of biological individual will perhaps derive from a theory of development, a conceptual tool of which we have at the moment only fragments at best (Minelli 2011).

## 2 Interaction Versus Inheritance

The second implication of Darwin's theory of microevolution brings us straight to Gould's major contribution to evolutionary biology.

This is the question of what identifies the level, or the levels, of selection. In Gould's interpretation, the correct reading of Darwin's work is that interaction is what matters, in the case of natural selection sensu stricto as well as in the case of sexual selection.

This view, however, has been notoriously challenged by Richard Dawkins (especially in *The Selfish Gene*, 1976) and by George C. Williams (*Adaptation and Natural Selection*, 1966), who have identified genes as the active and fundamental agents of natural selection, because genes are the elementary units of replication.

This shift from viewing selection as based on interaction to viewing selection as based on inheritance was one of the darkest *bêtes noires* against which Gould has being fighting over the years.

In his magnum opus on *The Structure of Evolutionary Theory* (2002), Gould explained at length (1) why the units of selection must be identified, *contra* Dawkins, in the units of interaction rather than in the units of inheritance, (2) why Williams' (1966) and Dawkins' (1976) efforts to construe all selection processes as inherently reducible to selection at the level of gene were based on a faulty reductionism where 'bookkeeping' takes the place of causality, and (3) why the whole theory of selection (and evolution) can be developed by reference to a single hierarchy of levels, or units, of selection, rather than to parallel hierarchies of units of interaction and inheritance as suggested by Eldredge (1985) and further elaborated by Williams (1992) in his later revisitation of the subject.

Gould acknowledged that Darwinian evolution requires that individuals must be able to pass their favourable properties to the following generation, but remarked that this requirement does not imply that units of selection must literally produce physical and complete copies of themselves. Instead, heredity only requires that units of selection be able to bias the genetic endowment of the next generation towards features responsible for the differential reproductive success of their parents: "genes would interact directly only if organisms developed no emergent properties—that is, if genes built organisms in an entirely additive fashion" (Gould 2002, p. 620).

## 3 Levels of Selection

Following an attack to the herd, an unlucky prey—possibly the weakest or the slowest member of the herd, or the one with the worst sight or hearing—falls under the predator's claws. The others survive the attack. The predator has thus acted as a selective agent in front of which the different individuals in the prey species' herd have shown their unequal fitness.

In this exemplary case, the unit of selection is the conventional individual organism. The same description applies when a ritualized fight between two rams assigns to one of them the right to mate in the current reproductive season, while denying it to its competitor.

Thus, if there is a question about levels of selection, this is apparently not about the existence, or the relevance, of selection at the level of the individual, but about the possible existence, or relevance, of additional levels. In principle, one may look for additional levels of selection both below and above the level of the individual organism (provided of course that the latter level can be actually recognized in the biological system we are considering). It seems legitimate anyway to question whether natural selection actually operates only at the level of the individual organism, the level on which Darwin and most of his immediate and later followers restricted attention, a restriction for which there seems to be no logical line of defence (Williams 1992, p. 38).

This is indeed not a new problem, and not necessarily a contentious one, but this area of evolutionary theory brings us straight to some of the most important concepts that Gould has been elaborating over the years, largely though joint work with his historical partners: Niles Eldredge, Elisabeth Vrba and Elisabeth Lloyd.

Smaller units involved in 'Darwinian' competition have been considered since the embryologist Roux (1881) proposed a view of the biological organism as a battlefield between parts, these being in turn molecules, cells and organs. Comparable scenarios of 'Darwinian' competition emerge again and again in developmental biology, a fresh example being provided by the demonstration that most of the cardiac muscle in the zebrafish heart is the progeny of a small percentage of the organ's founder cells—of those capable of more rapid and effective proliferation (Gupta and Poss 2012). One may dispute, however, whether in these cases the formally Darwinian scenario is more than just a convenient metaphor—whether it is indeed a real example of evolution by natural selection.

Already in the time of the ‘eclipse of Darwinism’ (Huxley 1942; Bowler 1983), Weismann (1896, 1903) was convinced that selection operates at multiple levels, that is, “among the biophors which form the protoplasm of the cell-body, among the cells of tissue, among the tissues of an organ, among the organs themselves, as well as among the individuals of a species and between species which compete with one another” (Weismann 1903, vol. 2, p. 119). Later, however, mainstream evolutionary biology has been increasingly focussing on the level of the individual organism and even an independent thinker like Waddington eventually dismissed the levels-of-selection debate of the 1960s as a rather foolish controversy (cf. Smith 1976, p. 277).

Theories of levels of selection other than the biological individual (e.g., Arnold and Fristrup 1982; Damuth and Heisler 1988; Grantham 1995; Michod 1997; Okasha 2006; Godfrey-Smith 2009) have flourished, however, in the last few decades, growing up from very different empirical and conceptual backgrounds. Eventually, Gould became involved in the corresponding debates both as a fighter against models centred on putative intraindividual units of selection (specifically, Dawkins’ selfish gene, as already mentioned) and as a strenuous defender of at least one kind of supraindividual units of selection, i.e., the species.

Eventually, acknowledging that selection operates at more than one level lead Gould to elaborate on the interrelationships among levels, a concern that explains his interest in developing and defending a hierarchical view of life.

Let’s examine this point more closely before returning to the issue of species selection.

## 4 Hierarchies

In general terms, a hierarchical structure of living world is traditionally accepted as granted (Okasha 2006), although some dissenting views have been occasionally voiced (e.g., Minelli 1998, 2009; Minelli et al. 2007). Against this widely shared traditional view, a diversity of questions can be addressed and very different metaphysical and/or epistemological perspectives can be defended.

In an evolutionary context, in particular, it may be sensible to discuss hierarchical organization from the perspective of the major evolutionary transitions (Smith and Szathmáry 1995), an exercise that translates into identifying a sequence of progressively larger and more complex (more heterogeneous) individuals, such as those enumerated by Michod (2005): from the solitary replicator (the gene), through the chromosome, to the individual cell, the multicellular organism and the colony.

According to Gould (2002), nested inclusive hierarchies are perhaps not a necessary, but a sensible framework for living systems. In his opinion, the biotic world would be different from the world we know, if a pervasive hierarchical organization would not support it—to the extent that we could not describe and understand it using our conventional ordering devices. However, he admitted that in nature there are exception to the principle of a fully nested hierarchy for evolutionary individuals. Among these exceptions, Gould (2002) listed the origin of cellular organelles by endosymbiosis. He regarded such events as "frozen" phenomena of history, quite remote from the main evolutionary forces acting today, but declared that he would have been ready to revise his views if lateral gene transport occurs as frequently as research was beginning to suggest in Gould's late years.

A different problem is, whether biology should recognize the existence of parallel hierarchies, of not. This brings us back to Dawkins' dichotomy between replicators and interactors, which essentially provides the foundation for Vrba and Eldredge's (1984) distinction between genealogical and economic hierarchies, a scheme on which Eldredge (1989) elaborated further with his idea of parallel hierarchies to separate the replicative and interactive criteria of evolutionary individuality.

Gould (2002) regarded the latter conceptual schema as an unnecessary complexity and offered two arguments to back his preference for a single-hierarchy model. The first was, that replication is a necessary but per se insufficient criterion for defining evolutionary individuality, thus it is not an adequate foundation for an independent hierarchy of life phenomena. Second, faithful replication (inheritance) represents one style of hereditary passage, but is neither a necessary mode on which to recognize evolutionary individuality or a criterion through which we can identify a unit of selection. Gould opted instead for a "single hierarchy—call it material, genealogical, or perhaps simply evolutionary—composed of interactors with adequate modes of plurification. These evolutionary individuals build a hierarchy of inclusion, with each higher level encompassing the individuals beneath as parts" (Gould 2002, p. 642, footnote).

## 5 Species Selection

In discussing about levels of selection, it may be useful to remark that is not just biologists who are interested in individuals, but also philosophers: as remarked by Ghiselin (1974, p. 536), "In logic, "individual" is not a synonym for "organism". Rather, it means a particular thing".

Back to biology, particular things are also species, and higher taxa. This is true, at least, if one accept the metaphysical views of Ghiselin (1974, 1997) and Hull (1976, 1978), that species (and higher taxa) are not classes, but individuals. This opens easily the door to a theory of multilevel selection: "Individuality wanders from level to level, so does the level at which selection can occur" (Hull 1980, p. 182). If so, why to deny the existence of levels of selection other than the individual organism? Still worse, why to contend that natural selection operates only at the level of the gene? "*A priori* preference for lower levels represents a claim for reductionism, not parsimony" (Gould 2002, p. 553).

In particular, if species are individuals, then species can be units of selection. With the remark, that to speak of species selection means to move into the domain of macroevolution. Let's remind that in Darwin's gradualistic view of evolution there was no scope for macroevolution as a distinct phenomenon, as everything was explained as the product of the steadily accumulation of microevolutionary modifications. In this context, even the distinction between simple intraspecific variety and 'true' species is distinctly blurred.

A first theoretical legitimization of species selection is found in a section on "the benefit of species" added by R. A. Fisher to *The Genetical Theory of Natural Selection* (Fisher 1930) in the second edition of the book (Fisher 1958). Let's add, however, that in this work the phenomenon was justified at the level of logics, but presented as questionable as matter of fact.

On the other hand, if Gould and Eldredge's (1971, 1977; also Eldredge and Gould 1972) model of punctuated equilibrium represents the actual, or prevailing mode of evolution, then species boundaries turn out to be less arbitrary than in the traditional Darwinian perspective, and species eventually emerge with an individuality that justifies looking at them as potential units of selection.

This is exactly why, within the framework of his theory of macroevolution, Gould regarded species selection as the most interesting level at which selection operates. I dare to say that eventually Gould became obsessed with species selection and this was probably the topic where his views evolved more conspicuously along his career. Two main phases can be distinguished in this intellectual journey, the first of which was marked by Gould's partnership with Elizabeth Vrba, the second by his joint work with Elizabeth Lloyd.

In his 2002 monograph, Gould characterized Vrba's approach to species selection as a view centered around the concept of "emergent character", i.e. "a trait functioning in species selection be[ing] emergent at the species level—basically defined as origin by non-additive interaction among lower-level constituents" (Gould 2002, p. 657). Gould and Vrba distinguished between the purely descriptive observation of "sorting", i.e. differential reproductive success, and "selection", i.e. the causal claim that the observed reproductive success is determined by the interaction between properties of the relevant evolutionary individual and its environment. Applying Vrba's criterion of emergent characters, Gould eventually counted differential species proliferation only as sorting at the species level: indeed, selection acts on characters of the individual organisms, although these characters have consequences at the species level by effect of upward causation. However, there are also emergent species characters upon which differential species proliferation may depend, and it is right these characters that identify selection at the species level.

However, he admitted that fully understanding species selection and eventually providing a definition for this concept was the most taxing job in his variegated career as an evolutionary biologist, causing him to publish erroneous interpretations and to repeatedly change his viewpoint. At first, that is at the time he and Niles Eldredge formulated the concept of punctuated equilibrium, he prepared himself to reformulate evolutionary trends in terms of differential species selection, rather than as examples of anagenesis within lineages. This perspective was already floated in Eldredge and Gould (1972) but fully developed only in Gould and Eldredge (1977) (see also Stanley 1975; Vrba 1980). At the time he applied the label of species selection to any pattern that admitted a description in terms of differential success of species, while these were treated as stable elements, under the assumptions of the theory of punctuated equilibrium. However, in his later critical view, this meant that selection was not perceived as different from simple sorting. In the 1980s, Gould moved to the opposite direction, restricting species selection only to cases based on characters emergent at the species level (Gould 1983; Vrba and Gould 1986). Eventually, he realized that this position was also too extreme and in his later work with Elizabeth Lloyd (Lloyd and Gould 1993; Gould and Lloyd 1999) he recognized emergent fitness as a conceptually broader, and empirically more testable criterion to identify species selection than emergent characters would have done, as the latter properly identified only a subset of instances of species selection.

Eventually, the individual organism and the species were singled out by Gould as the most important levels of selection, in an ascending hierarchy that begins with the gene and proceeds through the cell, the individual organism, the deme and the species. Gould was not sure whether independent and effective levels of selection exist beyond the species, and in his 2002 book still refrained from committing himself to the idea that clade selection plays a major role in evolution. In this expanded view of natural selection, the species becomes the unit of macroevolution, similar to the role played by the individual organism in microevolution.

## 6 The Evolving Rules of Evolution

A keen theorist of evolutionary phenomena like Gould could not fail to perceive the contingent nature of biological systems, and also of the overall hierarchy into which he regarded them to be organized. He remarked (Gould 2002) that the evolutionary hierarchy is not the product of structural or logical principles but has been historically deployed, in an a priori impredictable, contingent manner. This means that species and complex organisms do not exist since the origin of life, but only came into existence following the inventions of sexual reproduction and multicellularity, supplanting a previous hierarchy (still to be found today among the asexual unicellulars) arranged along the four levels of the gene, the cell, the clone, and the clade.

As reported above, Gould (2002) admitted that “nature presents some exception to the principle of a fully nested hierarchy for evolutionary individuals”, and cited with full approval Buss’ (1987, p. 188) remark, that “the major features of evolution were shaped during periods of transition between units of selection.”

Recent advances in fields as diverse as symbiosis, lateral gene transfer and the evolution of development suggest that to shoehorn biological systems into the levels of the so-called evolutionary hierarchy means to opt for an oversimplification of the complexity of life phenomena. Even the concept of individual organism, as a physically independent unit with its precise origin in time does not apply so easily and universally as generally accepted. Evolution, indeed, is not simply matter of change of 'individuals,' at any and all levels of the gene-to-clade hierarchy, but also matter of change of the units (or levels) of selection and of the rules of change themselves.

On a similar vein, Okasha (2006) remarked that the building blocks of the Neodarwinian view of evolution are themselves the product of evolution. This is true of the mechanisms ensuring fidelity in the transmission of genetic information from cell to cell (generation to generation), and of the genetic code itself (Godfrey-Smith 2000; Griesemer 2000).

## 7 Who Cares for These Conceptual Issues?

No physicist would arguably deny the importance of Galilei, Newton or Maxwell, but I guess we would be extremely surprised if we would ever find a scientific contribution by one of these authors being mentioned, not to say explicitly discussed or tested experimentally, in a paper published today. Things are very different in the case of Darwin, and also perhaps of Stephen J. Gould. There is a widespread misunderstanding, even among educated people, about the nature of studies on biological evolution. Many people imagine that evolutionary biology mainly revolves about discussing whether, or to which extent, Charles Darwin was right. Nothing, however, would be more distant from the actual course of scientific research in this area. Similar to physics, where Newton's *Philosophiae naturalis principia mathematica* are far from being a privileged target of study, evolutionary biology is largely insensitive to the debate, partly philosophical, partly purely of historical exegesis, eventually continuing in other corners of our intellectual arena. To same extent, this is also true of Gould, and of the aspects of evolutionary theory I have briefly mentioned in these pages, including whether we should recognize one or more levels of selection.

I have tried to get a quantitative measure of the relevance of the debate on the levels of selection among the community of researchers who attend the annual meetings of the Society for the Study of Evolution. Summing together the numbers of oral and poster presentations, at least one thousand contributions are presented every year at those meetings. How many among the presentations of the last few years deal with the levels of selection, with multilevel selection in particular? The number of such talks or posters is vanishingly small. Browsing through the abstract volumes of the last two editions, I found only three contributions (Johnson 2010; Nunney 2010; Goodnight 2011) where these words are mentioned in the title.

The apparent silence of professionals on these aspects of evolutionary theory to which Stephen Jay Gould devoted a large part of his immensely productive career must not be construed as a proof that he spent so much time and effort on questions of marginal relevance. Right to the contrary, his books and articles have been uniquely useful in educating people to think about micro- and macroevolution, selection and speciation, adaptation and exaptation. To fire new debate around these questions, we need the rare vision and the argumentative strength of people like him.

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# Beyond Spandrels: Stephen J. Gould, EvoDevo, and the Extended Synthesis

**Gerd B. Müller**

**Abstract** In evolutionary biology, the term "spandrel" infallibly elicits the memory of Steve Gould. It has become a standard in referring to constructional byproducts and developmental constraints. More often than not, these were regarded as lesser facets of evolutionary change, with priority given to population dynamics and the workings of natural selection. But the fundamental criticism, in the spandrels paper and other works of Gould, of the absence of organism level factors in the standard Modern Synthesis account, also helped trigger the EvoDevo revolution and important reconceptualizations of evolutionary theory. Recent versions of theory expansion include many of Gould's propositions but also theoretical changes emerging from other fields, such as genomics, non-genetic inheritance, niche construction, and others. These amount not merely to a numerical addition of factors to be taken into account, but also initiate major shifts in theory structure. As a consequence, today's extended frameworks of evolutionary theory entail a significant increase in explanatory capacity and predictive power.

## 1 Introduction

The origin of Evolutionary Developmental Biology (EvoDevo) in the 1980s is often associated with a methodological breakthrough: the isolation of major regulatory genes and the visualization of their expression patterns in developing embryos, which had opened up the comparative study of gene regulation. The preceding considerations that had prepared the conceptual frame for integrated developmental and evolutionary studies are mostly neglected, and so is Steve Gould's influential role in this process. Many of the evolutionary phenomena

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Gould evoked in his critique of adaptationism, such as non-gradual events, biased variation, non-adaptive traits, phenotypic novelty, and other forms of organismal change, now find—at least partial—solutions in the recognition of specific properties of evolving developmental systems. The research field of EvoDevo has rapidly expanded and has generated numerous empirical and theoretical approaches to reveal the contributions of development to the evolution of organismal complexity. The consequences of these endeavors for the standard evolutionary framework were a major concern of Gould's and are probably more far reaching than even foreseen by himself. In concert with theoretical innovation in other areas of evolutionary biology, EvoDevo elicits a reorganization of theory structure and a reinterpretation of the role of natural selection. In this chapter I am going to address some hallmarks of this theory shift and Steve Gould's fundamental contributions to it.

It is difficult to recall today how frowned upon any allusion to developmental arguments in evolutionary explanation had been in the decades preceding EvoDevo. "There are still those who would Haeckel biology" ran a characteristic commentary (DuBrul 1971) on early adepts of "ontophyletics," because recapitulation then was the only apparent way in which the ontogeny-phylogeny relation could be envisioned, and recapitulation was widely thought to have been proven wrong. Adaptive thinking reigned supreme, natural selection was the sanctioned explanatory principle, and population genetics the proper methodology to demonstrate its workings. In this context, development was regarded as an extended, if complicated, gene activation event, but the general notion among evolutionary connoisseurs was that "the details of the embryonic developmental process, as interesting as they may be, are irrelevant for evolutionary considerations" (Dawkins 1976). In these dogmatic times of evolutionary thought, Stephen Gould was one of the very few to argue with authority and eloquence that this was not all there was to development. His 1977 volume "*Ontogeny and Phylogeny*" convincingly demonstrated this point to an astounded evolutionary audience.

## 2 Gould's Early EvoDevo Reasoning

"*Ontogeny and Phylogeny*" took up themes that had been developed in the nineteenth century in contrasting ways by Carl Ernst von Baer and Ernst Haeckel, authors who were confidently considered outdated at the time of Gould's writing. He showed that with the rejection of universal recapitulation in the mid twentieth century, an important mechanistic principle for how evolution was able to modify developmental processes had been overlooked. It was not a law-like repetition of phylogenetic stages during ontogeny that mattered, but the mechanism that could generate evolutionary shifts of developmental timing: heterochrony. Even though Gould sided with von Baer, casting Haeckel in unfavorable ideological light (for largely unfounded reasons; cf. Richards (2008)), he reestablished Haeckel's concept of heterochrony as a valid scientific theme. Expanding on de Beer's (1930) categories of relations between ontogeny and phylogeny, Gould elaborated a new classification of heterochronic processes. He went on to illustrate their ubiquitous importance in evolution and coined his own "clock model" of heterochrony, which concentrated on the evolutionary dissociation between size and shape.

*ontogeny and phylogeny* had a considerable impact on evolutionary thought at the time, restoring development to evolutionary biology, and would eventually become seminal, together with several other volumes in the early 1980s, in the launching of EvoDevo as a discipline (Müller 2008). One of its immediate effects was the stimulation of first methodologies for how to approach the development-evolution interface in more formal ways. In one of these endeavors, headed by Pere Alberch, Gould took part in developing a quantitative and dynamical method for describing heterochronic events, based on the rates and relative times of the onset and offset of developmental processes (Alberch et al. 1979). The goal of this work on "ontogenetic trajectories," as Alberch had called the transitions in developmental morphospace, was a classification of the possible rules through which quantitative changes in developmental timing may influence and direct phenotypic change. Subsequent work provided empirical support for this approach (Alberch and Alberch 1981).

The conceptualization and later formalization of developmental constraint was another area in which Gould preconfigured EvoDevo (Gould 1980, 1989; Edwards 2008). Whereas conventional evolutionary wisdom had tacitly assumed the existence of constraints on the generation of phenotypic variation, it rarely paid explicit attention to their nature or their true evolutionary consequences. Gould demonstrated that without understanding the constraints imposed by established developmental systems it is not possible to explain the kinds of variation that can arise or, for that matter, cannot arise in a given organismal lineage. Actually, he would argue that even before elaborate developmental systems were established, the possible interactions within and among early multicellular assemblies dictated the morphological outcomes that would become exposed to natural selection, a view that receives much support from recent work on dynamical patterning modules (Newman and Bhat 2009). Hence the panoply of bodyplans generated in the Precambrian and Cambrian radiations may be much more a reflection of developmental constraint rather than genetic variation. These considerations were underlying Gould's thought provoking interpretation of the Burgess shale fauna and his views on the origins of body plans.

In yet another, if related, conceptual domain Gould once more pointed to development (and structural integration) as the decisive evolutionary factor. He argued that organismal form generation would necessarily produce structures that were not adaptive in origin but emerged as constructional byproducts, which would become adaptive only secondarily. The famous spandrels paper, coauthored with Richard Lewontin (Gould and Lewontin 1979), made this point and stirred a whole new discussion about the possibility and plausibility of non-adaptive traits. Of course that paper had much larger goals. It not only meant to expose the overarching adaptationist bias that dominated Anglo-American evolutionary thought at the time (which the authors suggested to remedy by infusing some

European “wholistic” thinking), but it also presented a number of alternatives to the adaptationist explanation. From the point of view of mechanistic causation, development was again in the foreground, especially the various kinds of correlational developmental effects, such as allometry, material compensation, or mechanically forced interaction.

By discussing these themes frankly in publications, lectures, public debates, and scientific meetings, Gould made the topic of development acceptable again at the evolutionary high tables, even though for a long time it earned little but ridicule from the Panglossian faction. His zeal may have been one of the crucial factors that lead to the Dahlem Workshop in 1981, probably the best date for the “official” starting point of what would become an astonishingly successful scientific enterprise: EvoDevo (the term itself born out of scorn). Stephen Gould had set the stage. Surely he was not alone and had a number of influential predecessors, such as C. H. Waddington, Gavin de Beer, John Bonner, and others, but in the 1970s there were not many well-respected evolutionary theorists who had a similarly outspoken penchant for development as Gould had.

EvoDevo rapidly gained momentum, developed its own methods and model systems and was significantly propelled by the application of molecular tools to comparative and experimental embryology. But the starting point had been theoretical. It had become clear—although certainly not universally accepted—that (a) not all of evolution was the steady, continuous, incremental kind of change prescribed by the Modern Synthesis, (b) not all organismal features were independently adaptive, (c) historical contingency was unaccounted for in the standard paradigm, and (d) the population approach had no theory for the evolution of structural complexity. A major deficit pertaining to the information flow relating genotype to phenotype had been exposed by Gould and his allies in the formal structure of the received theory: the absence of the rules of development. Gould had proposed several properties of development from which such rules could be derived, most prominently among them heterochrony, developmental constraint, and constructional byproducts (spandrels). What remains of these foundational concepts today?

## 3 Present Uses of Gould’s EvoDevo Concepts

Since Gould’s writings and the equally strong advocacy by Raff and Kaufman (1983), heterochrony has been expanded into a powerful theoretical framework (McKinney and McNamara 1991; Parichy et al. 1992; West-Eberhard 2003). Heterochrony, in the sense of relative shifts in the onset, offset, or rates of developmental processes, has been documented to occur in all major taxa (McKinney and McNamara 1991) and at all levels of organization, including molecular and genetic levels (Kim et al. 2000). Genes that affect the timing and rates of development, originally postulated already by Goldschmidt (1940), have been demonstrated in animals (Ruvkun and Giusto 1989; Ambros 2000) and plants

(Dudley and Poethig 1991), and genetic heterochrony effects have been experimentally tested (Zakany et al. 1997). Without doubt heterochrony based on gene regulatory changes represents a powerful mode for altering morphological characters and bodyplans. Furthermore, many of the direct effects of environmental influences on embryo development are known to act via timing and rate changes affecting different parts of life history (West-Eberhard 2003; Gilbert and Epel 2009).

In contrast to these supportive findings on process-related heterochrony, the use of heterochrony in the sense endorsed by Gould, namely as the age dependent dissociation of size and shape, has been less productive. Few empirical studies made successful use of the clock model he had proposed, and indeed the concept was criticized for being untestable in principle (Mitteroecker et al. 2005). In particular, the reliance of most shape comparisons on bivariate allometric traits hampers the conclusive inference of phylogenetic heterochrony, because it is always true for the standard bivariate case. Modern studies of multivariate examples show that shape space based heterochronies can be studied appropriately only with multivariate tools (Mitteroecker et al. 2005) which would permit to distinguish phylogenetic heterochrony from other forms of timing changes. But even advanced geometric morphometrics, which relies on multiple landmark comparisons, rarely provides a clear picture of size and shape dissociation. In this kind of approach a distinction of heterochronic phenomena that are simply a consequence of other changes in development from those cases in which heterochrony represents the causal mechanism for the evolutionary modification of a trait remains difficult.

The second conceptual domain made popular by Gould's promotion, *developmental constraint*, had been seminal in the foundation of EvoDevo, because it pointed to empirically testable properties of developmental systems that had the capacity to bias or limit phenotypic variation. Gould was not just a rhetorical advocate of constraint but himself carried out extensive empirical studies, especially on the West Indian land snail genus *Cerion*, in which he described a trade-off relationship between whorl size and whorl number that results from coiling and growth allometry (Gould 1989). Other conceptual treatments elaborated constraint theory (Maynard-Smith et al. 1985; Zelditch et al. 1993), and further empirical evidence was provided by comparative morphology (Bell 1987; Vogl and Rienesl 1991; Caldwell 1994), experimental embryology (Alberch and Gale 1985; Webb 1989; Streicher and Müller 1992), plant biology (Donoghue and Ree 2000), quantitative genetics (Cheverud 1984; Rasmussen 1987; Wagner 1988), and genomics (Roux and Robinson-Rechavi 2008).

Whereas early treatments of constraints concentrated on their limitational role, later works increasingly emphasized their facilitating effects on phenotypic variation and enhancement of the variational potential of a taxon (Kirschner and Gerhart 1998). It has been controversially discussed whether a taxon's capacity to generate phenotypic variation may also require a potential to relax or overcome established constraints (Wagner and Müller 2002). The recent literature shows that despite the unequivocal effect of development constraints on the rate of multivariate phenotypic evolution, many peripheral characters, such as butterfly eyespots, can be relatively little constrained (Beldade et al. 2002). By contrast, the interrelation of constraint with developmental plasticity, the topic sometimes thought to capture the essence of the evolutionary roles of development, harbors the possibility that direct effects of environmental conditions on developmental parameters may further enhance the generation of selectable variation (Fusco and Minelli 2010).

The third issue, *spandrels*, the non-adaptive byproduct concept suggested by Gould and Lewontin (1979), has often been considered a mere academic critique of adaptationism. Not much attention had been paid to possible mechanisms that could underlie so-called spandrel formation, until EvoDevo imbued this abstract concept with developmental process-based meaning. Today, the spandrel effect is most explicitly recognized in the various notions of evolutionary innovation and novelty. Novelty generation is thought to represent one of the main areas in which EvoDevo can make a genuine contribution to evolutionary theory (Müller 2007; Moczek 2008; Hallgrimsson et al. 2012). This is based on the recognition (explicit or implicit) that the origination of novelties represents a category of organismal transformation that is not addressed by the standard Darwinian account of steady and incremental variation. Gene network theory and its application to regulatory circuits, metabolic networks, and macromolecules indicates that similar concerns riddle microevolution (Wagner 2011).

Regarding the origin of novelty, a proposal much in tune with the spandrel effect is epigenetic innovation, the idea that developmental systems do not merely translate genetic variation into phenotypic variation but also represent an autonomous response apparatus that can elicit other forms of change. Natural selection, environmental induction, or other factors acting on overall organismal features, such as shape, proportion, function, or behavior, can provoke epigenetic consequences that arise from the generic properties of developing cell and tissue systems. Directional selection, for example, on developmental parameters such as cell number, blastema size, inductive interaction, or mechanical load meets threshold limits at which the response of the system will no longer be a linear one. It is at this point at which new structural elements, skeletal parts for instance, can arise as a side-effect of the evolutionary modification of developmental parameters and may only secondarily become exposed to natural selection. Thus, epigenetic innovation (Müller 2010) can have a significant role in the origination of first organismal bodyplans, structures, and form (Love 2003). In addition to the spandrel effect at the constructional level, the innovation concept includes the dynamical properties afforded by developing systems.

In short, EvoDevo has further developed and transformed some of the initial concepts introduced by Gould and others and has added new ones: gene regulatory evolution, modularity, evolvability, systems drift, plasticity, to name but a few. The overall theoretical framework of EvoDevo has matured and expanded, but the debate continues about how this affects the general structure of evolutionary theory. Gould had argued for a “revised and expanded” theory, which he sometimes even called a “new” theory, and in the early 1980s he was still optimistic that a major theory change was under way (Gould 1980). What did he actually mean by “revised and expanded;” how radical were his proposed alterations; did they represent a major challenge to neo-Darwinism; and how does his proposal compare with current trends in theory expansion?

## 4 Extending the Synthesis

Gould had great command of evolutionary theory. He castigated the Modern Synthesis, dating from the 1930s and 1940s, for its exclusive concentration on adaptation and regarded its gene centrism as a major fallacy. His version of an expanded theory was based on a hierarchical understanding of evolution, taking place simultaneously at different levels of organization, with different factors effective at each of these levels, from molecules to populations. This led him to propose two significant deviations from the canonical model: One concerned the ways in which heritable variation is produced, and another the mechanisms through which variations become fixated in a population. In the former he diverged from the standard view in not attributing the generation of phenotypic variation to genetic mechanisms alone. Instead he included a suite of higher order factors effective in the developmental and structural realm, the principal ones of which were described above, namely heterochrony, constraints, and spandrel effects. With regard to the second point, the fixation of variants in populations, he strongly argued for a multilevel theory of selection, acting at individual but also at supraindividual levels. Macroevolutionary forms of change, in particular, would not arise from gradual, adaptive transformations, but from higher-order selection operating upon groups and species. He also assigned an important role to the principle of cooption of traits that had evolved for a different purpose, a mechanism Gould and Vrba (1982) called exaptation, as well as to the representation of lawfulness based on historical accident, i.e., contingency.

A third significant departure from the standard evolutionary model appears in Gould’s treatment of speciation. As is well known, he challenged the dogma of phyletic gradualism inherent in the Modern Synthesis, according to which new species would only arise from steady, incremental, adaptive transformations of populations. Based on thorough studies of the fossil record, Niles Eldrege and Stephen Gould proposed the Punctuated Equilibrium theory (Eldredge and Gould 1972), which allowed for geologically instantaneous speciation events, followed by long periods of stasis. This theory and its subsequent elaborations represent the core of Gould’s expanded evolutionary framework, as it established macroevolution as an independent theoretical domain. It provoked a fierce and long lasting debate on the relation between microevolutionary mechanisms of variation and macroevolutionary patterns of speciation, but despite the mass of data in favor of punctuation it is still regarded as an exception rather than the rule. The details of Punctuated Equilibrium are discussed elsewhere in this volume.

Today, when a pluralism of factors has become more acceptable in evolutionary theory, Gould's proposals for an expanded theory don't seem so controversial, but at the time when he first expressed these views, together with others who argued in similar veins, they represented a major challenge to the prevailing orthodoxy. The population-genetically oriented evolutionary establishment was much irritated. All had looked so well. Incremental genetic change would have accounted for all variation in phenotypes and populations, and the discovery of DNA and of mutational mechanisms seemed to provide the necessary confirmation. Everything fell into place. But Gould, while embracing the core Darwinian logic, explicitly rejected the primacy of the gene in explaining organismal change as well as the encompassing and privileged role of natural selection assigned by the "hardened" theory. Gould's version of an expanded theory centered on the organismal level of evolution. As he emphasized in his writings, the explicit goal was to reestablish "the organism" to evolutionary theory, the core explanandum that had altogether been replaced in the Modern Synthesis by abstracted genetic effects. This was a bold step forward, but at the same time, while focusing so much on the organismal level of evolution, Gould remained curiously impervious to other theoretical developments that impinge with equal strength on the structure of evolutionary theory, such as behavioral and cultural evolution.

Recent versions of theory expansion include many of Gould's propositions, but go beyond them in several important aspects. As discussed above, EvoDevo has added heterochrony, constraint, and innovation, but it also added models of gene regulatory evolution, developmental systems drift, facilitated variation, and more. Besides EvoDevo theory, the latest scenarios of theory expansion comprise concepts that were not part of Gould's universe, such as genome evolution (Bernardi 2005; Koonin 2008), several forms of non-genetic inheritance, including epigenetic, behavioral, and cultural inheritance (Danchin et al. 2011), as well as the powerful theory of niche construction (Odling-Smee et al. 2003). Multilevel selection, with several forms of supra- and infra-individual selection, is equally recognized (Wilson and Wilson 2008), though still contested by some. Open minded theorists even accept direct effects of non-selectional factors on development, such as represented by the principle of environmental induction (West-Eberhard 2003; Gilbert and Epel 2009). The integration of these and other factors into a revised evolutionary framework has sometimes been called "expanded synthesis" (Kutschera and Niklas 2004) or "extended synthesis" (Pigliucci and Müller 2010). Not all expanded theory versions are explicitly designated as such, but since their concepts are used in the daily practice of evolutionary biologists, acceptance of a theoretical framework that is wider than the basic Modern Synthesis is implicit.

This does not mean "anything goes," but the recognition of a pluralism of factors acting at multiple levels of the evolutionary process, and with shifting relative importance, is a hallmark of current evolutionary understanding. Expanded conceptions accept that phenotypic variation is not only determined by mutation of individual genes and their frequency changes in a population but also by events affecting larger entities of the genome, such as gene duplication, horizontal transfer, and other genomic mechanisms. In addition, historically acquired and lineage specific developmental system properties are taken to determine the genotype-to-phenotype relationship, and instead of a singular, genetic inheritance system, multiple inheritance factors are taken into account. Natural selection at the organism level is supplemented by infra-individual and supra-individual selection mechanisms. And the initiation of phenotypic variation and innovation is not necessarily always through natural selection but may also result from direct influences of the environment on organismal development. Specifics of this summary overview can be found in recent collections, such as Pigliucci and Müller (2010). The purpose here is not to explain these concepts in detail but to discuss the theoretical consequences of including them into the evolutionary framework.

As Gould (2002) points out in his magnum opus, a new synthesis is still much in progress. In fact, as with all scientific theories, evolutionary theory always continues to progress (Pievani 2011) and, at any one point in time, must be regarded as the "current understanding." Historian that he was, Gould would have appreciated that this understanding has further progressed since his writings. However, the new pluralism of evolutionary factors is not merely a quantitative addition but also affects the logic and structure of the evolutionary argument. What are the main points in which the structure of the classical theory is altered under Gould's and subsequent attempts for theory expansion?

## 5 Shifts in Theory Structure

*The Structure of Evolutionary Theory* is Gould's comprehensive synthesis of his life-long critical examination of evolutionary theory and of his own contributions to what he called "modern versions" or "revisions" of the theory. He asserts that despite innovations in most elements of the theory, the core Darwinian logic remains intact and then proceeds to discuss the details of the changes as he perceives them. He explains the powers of a hierarchical theory of selection, the role of punctuated equilibria in macroevolution, and the workings of historical and structural constraints, but his views on how this actually affects the structure of the evolutionary argument are difficult to discern in the copious text. I will therefore try to briefly characterize the consequences of an expanded theoretical framework, pertaining to Gould's and also to more recent versions.

Let us depart from the standard logic of the Modern Synthesis theory, which—in condensed form—runs as follows (Fig. 1a): Individual phenotypes in a population differ due to genetic variation that arises randomly and at constant rates; all evolutionarily relevant inheritance is genetic; populations evolve by changes in gene frequency brought about by natural selection (plus flow and drift); the resulting variations of the phenotype are slight and incremental; variant phenotypes have different survival and reproduction rates in different environments; natural selection, affecting differential reproduction due to conditions external to

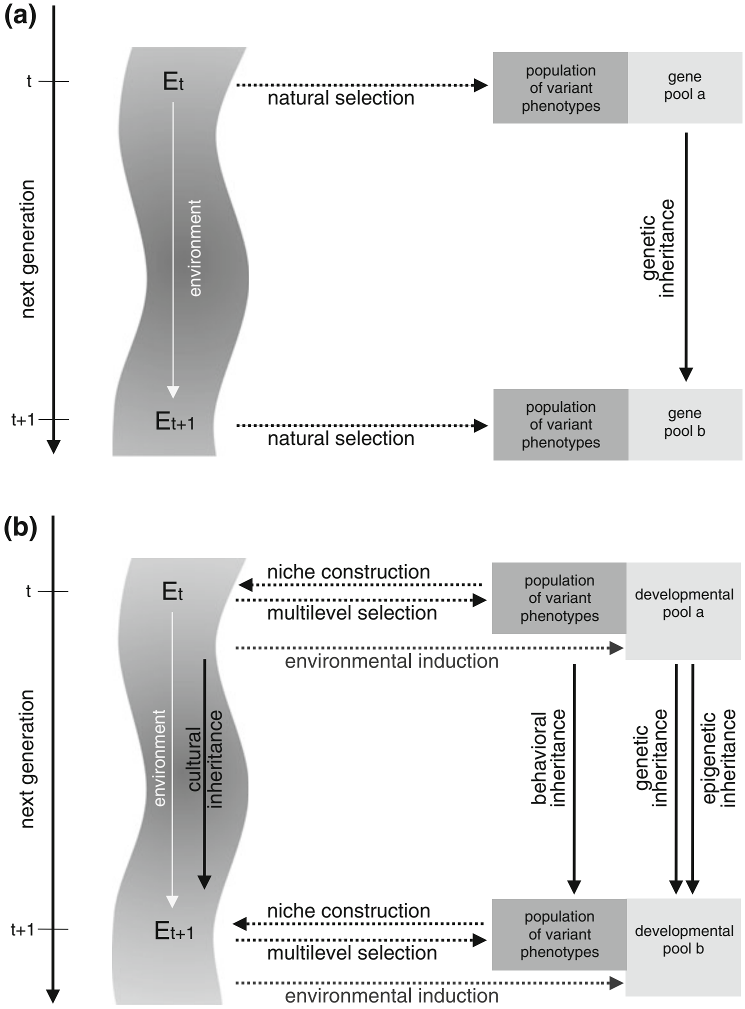

**Fig. 1** Diagrammatic representation of the shifted structure of evolutionary theory. **a** Modern Synthesis theory (after Odling-Smee). **b** Extended Synthesis theory. Explanations in the text

the individuals of a population, is a sufficient descriptor for all directionalities in phenotypic change; most characters are independently adaptive.

In extended frameworks several of these ingredients are revised or replaced by improved theory elements and additional interactions (Fig. 1b). The exclusive role of the genes (gene pool) in determining phenotypic variation in a population is replaced by shared developmental systems properties (developmental pool), obeying rules captured by EvoDevo theory. Single level natural selection gives way to multilevel selection, and the unidirectional relation of phenotypes with the environment (natural selection affecting reproductive dynamics via external conditions) is superseded by a reciprocal logic (activities of the organisms shape the environment which will be selective for subsequent generations). Inheritance between generations is no longer via genetic determinants alone, but is equally determined by several non-genetic factors—epigenetic, behavioral, and cultural. Furthermore, phenotypic variation at the population level is not exclusively shaped by selection processes but can also be elicited through direct influence of the environment on developmental systems.

The modified structure of the revised account has a number of general consequences. Under the influence of EvoDevo, for instance, evolutionary theory has become distinctly less externalist. Including the propensities of developmental systems shifts the weight of explanatory power from external to internal factors and from a unidirectional relation to a systems dynamic (Callebaut et al. 2007). At the same time the extended framework is less gene centered. A distinctly more pluralistic attitude prevails, allowing for non-programmed, non-genetic factors to influence the generation of phenotypic variation. Furthermore, due to multilevel interactions involved in all processes, emergent phenomena and discontinuities of the phenotypic outcome are not only possible but inevitable and thus provide support for punctuated dynamics of speciation. Overall, the pervasive adaptationism of the Modern Synthesis theory is overcome through the recognition of various non-adaptive mechanisms, such as the spandrel effects of Gould's or the consequences of genomic variation (Koonin 2008). It even appears that for certain forms of change a distinction must be made between mechanisms of variation and mechanisms of innovation, adding to variation a new principal form of evolutionary change. As Gould had desired, all these aspects of the revised theory emphasize the organismal dimension of evolution (Callebaut et al. 2007).

What appears to emerge as the most salient feature of these endeavors, whether Gouldian or post-Gouldian, is the revised role assigned to natural selection in the evolutionary logic. Whereas in the traditional account natural selection was the all powerful factor responsible for any specific solution attained by the evolutionary process, in the extended account that interpretation has shifted: Natural selection is maintained but has become more of a general boundary condition that is always at work, whereas the specific causality for particular phenotypic solutions is attributed to the realizing mechanism of development. In this view, selection per se does not produce phenotypic change, but is better interpreted as a releaser of developmental potential, producing emergent results that can subsequently become refined and fixated. Genes are interpreted as followers in this process (Jablonka 2006; Newman and Müller 2006; Schwander and Leimar 2011) serving to harness and streamline the effects of multiscale development. This vindicates earlier notions that saw selection acting "neither on the phenotype nor on the genotype, but rather on the emergent properties of developmental systems" (Alberch 1991).

In future discussions it could be useful to make a distinction between a "General Theory" and "Special Theories" of Evolution (in a sense similar to, but not identical with, Webb's (2011) proposal, as it is here meant to apply to living systems alone). The General Theory concerns the mechanism-independent, overall principles that underlie the kinds of biological change termed "evolution," i.e., the dynamical relationships between variation, inheritance, and replication of organisms and their traits. Special theories, by contrast, explain the features of evolution by specific mechanisms, as in the case of the Modern Synthesis (MS), a special theory in which genetic variation and natural selection are used to explain phenotypic variation and adaptive dynamics. It is concerned with a subset of both, evolutionary phenomena (variation, adaptation) and mechanisms (genetic change, natural selection). Extended theories, in the sense discussed above, are special theories that use a different and enlarged set of mechanisms to explain these same phenomena, plus additional ones. The Extended Synthesis (ES) proposal (Pigliucci and Müller 2010), for example, includes a suite of additional genomic, epigenetic, developmental, behavioral, and cultural mechanisms and applies to both adaptive and non-adaptive as well as non-variational phenomena. Because of the unequivocal empirical and theoretical evidence that some of the specialized assumptions of the MS (such as genetic exclusivity, externalist selection, or panadaptedness) are not an adequate explanation of organismal evolution, the ES supersedes the MS as a special theory, but not as the general theory. Other expanded theory versions have similar special theory status (Kutschera and Niklas 2004; Koonin 2008; Depew and Weber 2011; Helanterä 2011; Huang 2011; Weber 2011; Wilson 2011; Schrey et al. 2012).

A new synthesis in evolutionary theory will not be declared. Rather it is going to naturally replace the received theory because of one significant property: its superior explanatory and predictive capacity. The extended theory framework applies to a number of phenomena the standard theory was unable to account for (such as biased variation, morphological innovation, non-adaptive characters, punctuated dynamics, etc.). At the same time its predictive power has increased. In particular, the extended theory permits predictions not only about which kinds of variations are going to be maintained in the evolutionary process, but also about which kinds of variations and innovations can arise under given conditions. The entrenched concentration on a restricted repertoire of evolutionary factors had stifled theoretical progress for a long time, but finally these limitations are overcome. We must be grateful to Steve Gould for having shown the way out of the deadlock.

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# Biological Complexity and Punctuated Equilibria

**Marcello Buiatti**

**Abstract** The theory of punctuated equilibrium proposed by Gould and Eldredge has been considered "heretic" isolated from the main currents of scientific thought for a long time. This paper challenges this view showing that, contrary to this position, acceleration of evolution and criticality are processes very well known in physics and in general in the field of complex systems. This thesis is supported by a vast number of examples of acceleration in living systems deriving from their state of extended criticality (Bailly and Longo) and new equilibria can be reached through the utilization of four categories of variation (genetic, epigenetic, behavioural, cultural) the last one being used by humans, the constructors of cultural punctuated processes. All these concepts, finally, are documented with a vast number of recent experimental data fully confirming the paleontological observations by Gould and Eldredge.

Living systems are "multi-verse", that is they show at the same time apparently contradictory features such as continuity and discreteness, chance and determinism, selection by the environment and according to internal rules etc. Rather unfortunately life sciences students often tend to think in terms of antinomies and are therefore liable to use "only one pair of glasses" when observing nature. For this reason conflicting theories have sometimes been developed on the ground of the same experimental data. This behaviour has been typical of the "Modern era" where the antinomy of chance versus determinism has been the background of opposite and often dogmatic theories. A paradigmatic "case study" of this kind of interaction between science and the cultural background of single scientists is the behaviour of the three Nobel Prize winners in 1965, namely Jacques Monod, André Lwoff and François Jacob, who had obtained the prize for their pioneering work on the regulatory system of the bacterial *lac* operon. Interestingly, although they had been working together under the direction of A. Lwoff, the head of their Department, they

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had strikingly different conceptions of living systems as shown by the three Nobel Prize lectures. Jacques Monod based his vision on the antinomy of chance vs. necessity (the title of his famous book published in 1969) as shown for instance by the following sentence: "One of the most relevant features of all living systems is to be objects endowed with a project. We should also say that living beings differ from the structure of whatever other system in the Universe because of this feature which we may call teleonomy… The structure of a living being is the result of a totally different process as it does not owe anything to the action of external forces… A third relevant feature of these objects: to be able to reproduce and transfer—*ne varietur*—the information needed for their structure… wholly conserved from one generation to another. We shall call this property "*invariant reproduction*" or, more simply, *invariance*… The structure… can be therefore autonomously and spontaneously realized without external contributions, without new information: Its epigenetic construction therefore is not a *creation* but *a revelation*… We can today deduce the general law: that of chance…chance is tapped, conserved and reproduced through the mechanism of invariance and transformed in order, rule, necessity… The whole system is wholly and deeply conservative…it defies any "dialectical" description. It is fundamentally Cartesian and not Hegelian: the cell is really a machine,…. The fundamental biological invariant is DNA" (Monod 1970). For Monod therefore living systems are not influenced by the dynamic environment being fully determined by a programme "written on DNA" as proposed back in 1942 by E.Schroedinger and stated as a "dogma" by Francis Crick in 1958 following his discovery with James Watson of the shape of DNA molecules in the crystallised state. The conception of life of Lwoff was very different: "An organism is an integrated system of interdependent structures and functions. An organism is constituted of cells, and a cell consists of molecules which must work in harmony. Each molecule must know what the others are doing. Each one must be capable of receiving messages and must be sufficiently disciplined to obey. You are familiar with the laws which control regulation. You know how our ideas have developed and how the most harmonious and sound of them have been fused into a conceptual whole which is the very foundation of biology and confers on it its unity… It is clear, on the other hand, that the expression of the genetic material is subject to external influences. Ten years ago, it still seemed possible that, in certain processes such as the induced biosynthesis of enzymes or of antibodies, the presence of specific compounds could modify the synthesis of proteins, mold their configurations, and hence alter their properties. What the study of regulatory circuits has shown is that the compounds in question serve only as simple stimuli: they act as signals to initiate a synthesis whose mechanism and final product remain entirely determined by the nucleotide sequence of the DNA. If the nucleic message may be compared with the text of a book, the regulatory network determines which pages are to be read at any given time." In other words Lwoff considered the living systems as networks of interacting components influenced by the environmental changes and therefore not governed by chance nor by necessity but continuously changing during their lives. Moreover, the dynamic fate of a living system derived in his opinion from the time-dependent activation by environment of the tools (the "pages") whose heritable information was carried in DNA. F. Jacob had an even more complex theory in his book *The Logic of Life* where he wrote: "Every living being, says Goethe, has in itself the reason of its existence: all the parts react one with another… Living organisms are subject to different influences by not living objects and other living beings… To cope with those actions an equal and opposite action is needed… in comparative anatomy a fragment is not anymore an isolated element: it is a sign of a whole organization… the relative relevance of an organ is measured through the constraints that imposes on the others… only combinations satisfying functional needs of life are allowed. Life is… a play of interactions of organisms and environment: it is the dialectic of the same and the different within a unitary history of nature… It is not the matter which evolves but rather the organization, the unit of emergence always capable to unite with other similar unities to become integrated in a system." It is difficult to understand ex-post why three scientists working together on a simple regulatory bacterial system and building a unitary model would diverge in such a manner on the conceptual generalization of their findings. The only possible explanation of this apparent contradiction may stand in the different cultural background of Jacob and Lwoff on one hand and Monod on the other as the first two were jewish of Russian origin while the third was French influenced by the Cartesian thought as he formally stated saying "I am not Hegelian but Cartesian". It is worth noting that the mechanistic view of life has been by far the most accepted paradigm in the modern era when the "spirit of times" identified the notion of a continuous human progress with the mechanisation of living and non-living matter according to human projects. The two main theories supporting this vision have been the "central dogma of molecular biology" based on the "informational metaphor", introducing the notion of a wholly deterministic programme "written on DNA" and the neo-darwinist theory of evolution coherently called by J.Huxley "The Modern Synthesis". The main tenets of this theory based on population genetics data are: (a) individuals are the subjects of evolutionary change and speciation occurs through a continuous change of the relative frequencies of discrete and independent factors (alleles and genes) randomly assorted at every generation as suggested by Mendel, a physicist close to a mechanistic current of thought whose conception of life was declared in the "Manifesto of medical materialists"; (b) genes and alleles functions are additive and therefore phenotypes are fully determined by the addition of the effects of alleles and genes without any influence by the environment; (c) the evolutionary change is due to three processes, namely, mutations (chance), random drift (total chance), natural selection (necessity) and, according to the more orthodox version of the theory by R.A. Fisher, evolution occurs in a stable environment ad proceeds according to a continuous dynamics moving towards the optimal adaptation according to an evident metaphor of progress. All through most of the twentieth century this conception was considered "the" theory of evolution although a number of "heretics" kept proposing different and more complex views as the already mentioned A. Lwoff and F. Jacob. C.H. Waddington challenged the gene-centric population genetics and asked for a "phenotype paradigm", R. Lewontin and I.M. Lerner showed that interactions between alleles in heterozygous organisms are not additive, S. Wright introduced the concept of fitness landscape, meaning by that the ensemble of different genetic complements in the same species liable to reach the same fitness average value, R. Goldschmidt showed that a single genetic change could induce striking modifications in development and coined the term "hopeful monsters" to describe organisms "trying" to gain a new equilibrium. B. Mc Clintock discovered in maize transposable elements (T.E.) liable to "jump" into genes thus causing unexpected changes in the phenotype thus disproving in advance the invariant nature of DNA proposed much later by J. Monod. In the same Cold Spring Harbour symposium of 1951 also Goldschmidt discussed his theory of speciation and accelerated evolution. In the words of Dietrich (2000): "Using two different models, Goldschmidt showed how different views of genetic structure and gene action could provide a mechanism for rapid speciation. Developmental systems were emphasized in one model and a hierarchy of genetic structures in the other". This model was known by Gould when in 1977 wrote: "Goldschmidt raised no objection to the standard accounts of microevolution; he devoted the first half of his major work, *The Material Basis of Evolution* (Yale University Press, 1940), to gradual and continuous change within species. He broke sharply with the synthetic theory, however, in arguing that new species arise abruptly by discontinuous variation, or macro-mutation. He admitted that the vast majority of macro-mutations could only be viewed as disastrous—these he called "monsters." But, Goldschmidt continued, every once in a while a macro-mutation might, by sheer good fortune, adapt an organism to a new mode of life, a "hopeful monster" in his terminology… as a Darwinian, I wish to defend Goldschmidt's postulate that macroevolution is not simply microevolution extrapolated, and that major structural transitions can occur rapidly without a smooth series of intermediate stages. I shall proceed by discussing three questions: (1) can a reasonable story of continuous change be constructed for all macro-evolutionary events? (my answer shall be no); (2) are theories of abrupt change inherently anti-Darwinian? (I shall argue that some are and some aren't); (3) do Goldschmidt's hopeful monsters represent the archetype of apostasy from Darwinism, as his critics have long maintained?." For Goldschmidt's, transposable elements provided a shining example of position effects and a dynamic genom. It is worth noting that Goldschmidt and B. McClintock had been working in the "forties" and "fifties" of the Twentieth Century, when the followers of the mechanistic conception of life were introducing the DNA-centric paradigm, the Watson and Crick model of DNA being published in 1953 and the "central dogma of molecular genetics" both in Nature by Crick in 1958 following Schroedinger's intuition of 1942. The scientific atmosphere started changing only after 1962 with the pioneering work by the physicist Lorenz (1963) on deterministic non periodic flow showing that small changes in a complex system could induce unpredictable re-organization of that system. This finding based on the pioneering work by Poincaré opened the way to a whole new branch of physics and, later on many other areas of thoughts from biology to philosophy, economics etc. The work of Eldredge and Gould (1972) introducing the concept of punctuated equilibria certainly were one of the very first responses of the new theories in biology as confirmed by Gould: "Complexity theory can help us to understand why prediction is so difficult…. I can tell you to the minute when the next eclipse is going to occur, because it's a simple system with limited interactions. I can't tell you where human evolution is going. Also, the mathematical analysis of complex systems composed of multiple, independent parts shows that a small perturbation can produce profound effects, because of the way it cascades through the nonlinear interactions of the system. If you then add a little bit of randomness you get profound and unpredictable effects… With Darwinian theory, there's no notion of general advance. There is adaptation to a changing environment. Darwinian theory is about constant local improvement, and since environments are always changing, especially given technological progress, there always has to be flexibility for adaptation". Gould was openly introducing the correlation of unpredictability and the dynamic connections between components of a system leading to "sudden" re-organization of the whole system after changes in "hubs" (highly connected elements). This conception is very near to that of physicists like Bak and Paczuski (1995), who wrote: "The basic laws of physics are simple, so why is the world complex? The theory of self-organized criticality posits that complex behavior in nature emerges from the dynamics of extended, dissipative systems that evolve through a sequence of meta-stable states into a critical state, with long range spatial and temporal correlations. Minor disturbances lead to intermittent events of all sizes. These events organize the system into a complex state that cannot be reduced to a few degrees of freedom. This type of "punctuated equilibrium" dynamics has been observed in astrophysical, geophysical, and biological processes, as well as in "human social activity". Biological systems, where connections between components is within and between the different levels of the hierarchical organization of life and with the environment are in a state of "extended criticality", in a continuous interplay between the different components of biological randomness (Buiatti and Buiatti 2008, Buiatti and Longo 2013). Therefore biological dynamic structures and processes are at the same time variable and constrained by what Charles Darwin probably would have called "correlated variations", a forgotten early challenge to the "chance vs. necessity" dogma proposed by Jacques Monod implying the co-evolution of network components and therefore the existence of external (environmental) but also "internal selection" as proposed by Whyte (1965), due to the need of coherence of changes with the "internal rules" of living systems. Both "internal" and "external" stress induced by changes in one or few components of one level of the hierarchical organization of living systems networks, from the molecules to the biosphere components, may cause "butterfly" effects liable to be transmitted to the other levels leading to punctuated equilibria as foresee bu Gould and Eldredge. The dynamic processes of change may then lead either to the death of the organism(s) or to genome "shuffling" processes and an acceleration of the evolution of the affected networks putatively leading to the survival of R. Gold-schmidt's "hopeful monsters". These concepts are now fully supported by genetic and molecular studies of the last decades and are part of a new vision of life, based on new disciplines such as epigenetics and mathematical/ computational methods for the study of complex biological system. We know now that the first reaction of living systems to the "stress" induced by both "internal" modifications and the environment, are the "burst" of genetic variability in bacteria and complex "genome shuffling" processes in eukaryotes both increasing genetic variability liable to be utilized under selection pressure for successful re-arrangement of connections between components of the genomes. I shall now discuss a number of examples of evolution acceleration through the increase in genetic variability following stress by the environment and/or by internal modifications of “key nodes” of genetic networks, translating into molecular terms what Gould and Eldredge have predicted on the ground of paleontological and morphological data. In the case of bacteria (Wright 2004) different kinds of stress induce the expression of RpoS, a gene coding for a sigma factor inactivating mismatch-repair genes such as MutS, MutL, MutH, and inducing others such as Dps, dinB, umuC, umuD, in general belonging to the Y family coding for error prone DNA polymerases (see for instance, Galhardo et al. 2007, 2009; Chiang and Schelhorn 2010). The processes leading to bursts of genetic variability in eukaryotes are more complex than in bacteria and may lead to all levels of “shuffling”, from exon shuffling giving rise to new proteins, to gross genome re-arrangements (genome shuffling) often due to the presence of mobile elements (see Shapiro 2010). Mobile elements, discovered by B.Mc Clintock as discussed earlier in this paper, are partially autonomous DNA sequences liable to replicate (transposons) or be retro-transcribed from RNA to DNA (retro-posons), “jump” and spread their copies in the genome (for instance they cover 45 % of the human genome). Transposable elements in eukaryotes (T.E.) are normally kept silent through epigenetic regulation with RNA interference, DNA methylation, histone modifications, to avoid harmful effects of their spreading throughout the genome putatively “breaking” relevant genes. However, (Zeh et al. 2009), the presence of stress disrupts epigenetic regulation and unleashes the mobile elements leading to an increase in genetic variability liable to help “hopeful monsters” to find new adaptive peaks. Stress effects on T.E. mobility have been discussed in (1984) by Mc Clintock, and now (see D. Zeh et al. 2009 for a thorough discussion), there is a vast literature on de-methylation, mobility and increased expression of transposons and retro-transposons following a wide range of stresses such as heat, tissue culture both in animals and plants, famine in humans, etc. The effects of transposable elements movement have been shown to happen at the cellular level as in the case of cancer cells and at the organismal level in specific cell lineages during development. It is worth noting that cells bearing T.E.- induced mutations during development will only seldom enter the reproductive cell lineages in the case of animals but, as discussed thoroughly by Buiatti (2011a), in plants cells belonging to the L1 and L3 embryonic cell layers may “colonize” the L2 devoted to the formation of the reproductive apparatus and therefore may affect the course of evolution. T.E.s and particularly helitrons, liable to induce gross genome re-arrangements, are most probably the reason why, as shown by Morgante et al. (2005), different maize cultivars, although belonging to the same species, may show unexpected genome differences. It is worth noting that genome re-arrangement is not only induced by stress induced by the environment but may derive from “internal” modification of the genomic network equilibrium due to single mutations with pleiotropic effects, to the horizontal transfer of single or few genes, interspecific hybridization etc. Pleiotropic effects are caused by mutations in genes connected with other members of a network at the metabolic or developmental levels. A very well-known example of genes affecting development is given by the mutations in homeotic genes of *Drosophila* shown to control the pattern of body formation of many animals, humans included. Edward G. Lewis hypothesized that the duplication and diversification of homeotic master regulators underlies the evolution of increasingly complex body plans and was awarded the Nobel Prize in 1995 for his discovery and the new vision of developmental processes deriving from it (see on this subject also Minelli 2013). Horizontal transfer may be due to a number of causes like infection, symbiosis, human artificial integration of genes with genetic engineering methods. An interesting example of the effects of the introgression of single of a few "alien" genes in plants on genome evolution is the integration of *Agrobacterium rhizogenes* genes in plants of the *Nicotiana* genus. *Agrobacterium rhizogenes* is endowed with a plasmid containing a set of genes known to influence the plant hormone system and, according to Naf (1958), there has been an ancestral horizontal transfer from the bacterium to many *Nicotiana* species in root cells, which however, as discussed elsewhere (Buiatti 2011a), were able to produce "genetically engineered" shoots and whole *Nicotiana* plants. Naf subdivided the genus according to the presence/absence of bacterial genes and showed that hybrids between species belonging to the two groups were tumour prone. As shown later by Bogani et al. (1997) and Intrieri and Buiatti (2001), the different "genetically engineered" species settled in different ecosystems, maintained different complements of bacterial genes and showed different hormonal patterns as also confirmed by their in vitro differentiation behaviors (Bogani et al. 1985). So, very few introgressed genes of bacterial origin drastically changed the evolution and differentiation of the *Nicotiana* genus through a complex interaction between the plant and bacterial genomes suggesting a co-evolutionary process. This hypothesis was confirmed by the comparison of the evolutionary trees of the bacterial genes present in plants with those of the same genes in present day *Agrobacterium* spp., showing that introgressed ones followed the *Nicotiana* genus evolution pattern, the second group evolving according to a strikingly different one (Intrieri and Buiatti 2001). To put this process in "Goldschmidtian" terms, the introgression of *Agrobacterium* genes produced a number of "hopeful monsters" a part of which survived through the selection of different gene complements followed by the concerted re-arrangement of both the "transgenes" and the host species genomes. Also in this case as in Goldschmidt's work, the introgressed gene(s) acquired the function of a new "hub" in the hormonal network of the plants, leading to a general re-arrangement of it and to the differentiation of the genus, although it has been suggested (Naf 1958) that a number of species "discarded" the bacterial genes during evolution. One of these bacterial gene free species, *N.langsdorffii*, offered an interesting example of successful re-arrangement when it was genetically engineered in our laboratory with a rat gene coding for the glucocorticoid receptor not supposed to interfere with the host hormonal system. To our surprise the plant hormonal network was drastically changed and the transgenic plants showed unintended morphological and physiological changes such as thin and thicker leaves, different life cycles, lower seed set, resistance to heavy metals, drought, heat and other abiotic stresses. It should be noted that first generation transgenic plants produced a low number of seeds but seed production recovered in the third generation (S. Giannarelli et al. 2010; Fuoco et al. 2013). While in the examples just discussed only one or few genes were integrated in wild type genomes and there is as yet no evidence of transposon movements following the genetic stress, the situation is different in the case of interspecific hybridization followed by allo-polyploidization, a basic process for natural plant speciation discussed in the pioneering paper by Stebbins (1950). As thoroughly discussed by Feldman and Levy (2011), in this case brand new interactions between the genetic components of the two species must be developed and for this reason, as shown already by Boyko et al. (1988) and discussed by Feldman and Levy (2011), a part of the original DNA of the two species is lost, epigenetic marks are changed modifying the expression patterns, transposons and particularly helitrons are released leading to genome shuffling, etc. Although fertile interspecific animal hybrids are very rare due to the low occurrence of fertile allopolyploidy, in a number of instances genome modifications have been reported also in this case (see for instance O’Neill et. al. 1998; Labrador et al. 1999; Brown et al. 2002; Metcalfe et al. 2007; Sakai et al. 2007). Summarizing the features of all the examples of evolution acceleration discussed so far, we can conclude that they all are induced by negative modifications of living networks due to internal and external causes, their recovery being based on “bursts” of variability obtained through different “tools” and processes in bacteria, plants and animals. Moreover, stress leading to punctuated equilibria may occur at all levels of the hierarchical organization of life from the molecular networks to the cellular ones, the organismal, the bacterial/cellular “super-organisms” like humans and their internal bacteria ecosystems, the Eldredge “avatars” in ecosystems, the biosphere. All this evidence fully supports the “sloshing bucket theory” proposed by Niles Eldredge (2008) who extended this kind of evolutionary dynamics to ecosystems and to the biosphere attributing to a process similar to what we have been discussing the appearance of a vast number of new species after extinction processes. Niles Eldredge, after a thorough discussion of his theory concluded that “The greater the magnitude of the environmental event, the greater the change in ecosystems, including the magnitude of diversity loss through extinction; the greater the loss of higher taxa, the more different will be the newly evolved taxa, and thus the nature of the succeeding ecosystems that replaced the prior disturbed systems”. At all levels of biological organization therefore, the first answer of the “disturbed systems” is the increase in variability, leading to the acceleration of evolution and the emergence of “winning hopeful monsters”. We should not forget however that the production of variability is possible only in the presence of positive selection of different sets of tools allowing the increase of different kinds of variation as discussed thoroughly by Jablonka (2004), namely genetic, epigenetic, behavioral and symbolic. We already discussed tools and processes needed for the increase of genetic variability such as the RpoS system in bacteria and transposon movement in eukaryotes, but we should also mention the existence of hyper-variable regions both in prokaryotes and eukaryotes for instance in immuno-globulins, but also cadherins and other proteins critical for the organization of synapses and many other. Particularly, bacteria mostly utilize genetic variability for adaptation taking advantage from their one-chromosome genome which allows the immediate usage of recessive adaptive mutations, the very frequent horizontal intra- and inter-specific transfer of DNA, their short lives and the consequent low number of environmental changes during single life-times to cope with. In other words prokaryotes are endowed with very high levels of evolvability while eukaryotes and particularly plants developed a large set of epigenetic tools allowing changes in gene expression during life time thus using mainly plasticity for adaptation. In animals the presence of a very refined and plastic nervous systems allowed the usage of a wide range of behavioral variation particularly complex in social systems, to be transmitted throughout generations often through trans-generational epigenetic processes (see again Jablonka and Lamb 2004 for a thorough discussion of this dynamics). Finally, humans, can be themselves considered an extraordinary example of acceleration of evolution from a putative "hopeful monster" state to the construction of an extremely powerful tool (the human brain), liable to produce an immense variability of adaptive behaviors. Differences between the organization of our brain when compared with those of other primates are striking. As thoroughly discussed by Blazek et al. (2011), the relative increase of the ratio between the encephalus and other brain components, now by far higher than in other primates, is only one of the many changes occurred in the internal structure of human brains. Just to mention some of them, there has been an escalation in the number of neurons, the differentiation of cortex areas, the formation of mini-columns, the spreading of mirror neurons systems, the configuration of cognitive neuron nets etc. At the same time only in the human line of evolution there has been an acceleration of changes in key genes such as the microencephalin one, the ASPM, a series of other genes correlated with brain size, the foxP group. critical for the communication, those related with the formation of the area of Broca, a number of genes coding for perception and recognition functions etc. Recently Haygood et al. (2010) have shown that changes in the above mentioned genes have occurred mainly in non-coding regions or had the information for transcription factors involved in recognition and regulation of gene expression. These results are in agreement with earlier ones by Arbiza et al. (2006), who found that human G-protein coupled receptors and sensory perception genes showed the highest divergence with chimpanzee's ones. Moreover, N. Lambert et al. (2011), with an innovative approach, analyzed differences in expression levels between humans and chimpanzees through the three-dimensional reconstruction of fetal brains at mid-gestation and compared expression patterns in the Broca ad Wernicke areas with those of associated areas thus showing that language-related areas have higher expression levels of accelerated genes. An obvious consequence of the just described changes in more than hundred human genes related to brain function has been the modification of the metabolic brain network as shown by Fuo et al. (2011), who analyzed the concentrations of more than hundred metabolites and found that 77 % of them differed between primate species, differences being fourfold in the human prefrontal cortex when compared with cerebellum in the human lineage. All these data suggest therefore a very specific acceleration of change in the human lineage, the vast majority of accelerated genes concerning brain relative dimensions and organization and recently developed (young) brain fetal and infant expressed genes, as proposed by Zhang et al. (2011), these genes being directly or indirectly bound to perception, signaling, language, neuron connections and organization during the early life. Moreover, Zhang et al. found out that many of the mentioned genes developed their sequences after the morphological origin of the neo-cortex and consequently proposed that a positive selection may have been the key process for their development during an amazingly short time in paleontological terms. As discussed in an earlier paper (Buiatti 2011b) in a short time the fast change of a limited number of key genes all active in the brain network drastically changed the adaptation strategy of humans as it allowed the construction of "mental" projects liable to be used to change the environment. Of course many other species and particularly social ones do change the environment but in a stereotypic way while humans may invent ever-different projects according to the transformation of the contexts. According to the philosopher Jonas (1994), this is possible because humans may use the knowledge deriving from inter-personal interactions to "imagine" new combinations of the data and concepts acquired and change the world according to the most adaptive ones. The "imagination" allows original descriptions of components of the context to painters as well as transcendent thought to the philosophers and theologians and the production of projects of adaptive modifications of the contexts to scientists and technologists. The capacity to actively change the environment according to adaptive innovative projects instead of being passive object of selection by the environment is the reason why genetic variability is much lower in humans than in the other primates although we are seven billions while our "cousins" can be counted in the range of thousands (Barbujani et al. 1997; Romualdi et al. 2002). Cultural variation and its diffusion through complex languages and now also computational tools are in other words by far the more powerful adaptation system existing on earth this being the reason of the entrance of the biosphere into the critical phase of the Anthropocene era (see Steffen et al. 2007), the last one of the human series of cultural punctuated equilibria.

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# Part III
# The Anthropological Legacy

# Stephen J. Gould's Intellectual Legacy to Anthropology

**Ian Tattersall**

**Abstract** It is rare for an invertebrate paleontologist and evolutionary theorist to make a significant impact in the rather insular field of biological anthropology. But in this case, as in so many others, Stephen Jay Gould was a shining exception to the rule. His contribution to anthropology was to a large degree an indirect one, accomplished through his contributions to evolutionary thought in general, and more specifically through his extraordinarily effective *Natural History* columns. But it was no less forceful for that. In a field in thrall to the "hardened" (his term) Evolutionary Synthesis, Steve's energetic promotion during the 1970s of the notion of punctuated equilibria opened up new perspectives leading to a more rational appraisal of the diversity evident in the human fossil record. And his tireless advocacy of the idea that human phylogeny presents us with a "bush" rather than with a "ladder" introduced into paleoanthropological thought a powerful and compelling metaphor that continues to gather momentum. His *Natural History* columns additionally covered anthropological subjects as diverse as bipedality as the fundamental human adaptation; the single African origin of *Homo sapiens*; the authorship of the Piltdown fossil hoax; the fate of the Neanderthals; the unity of mankind; and nature versus nurture and the relationship of race and IQ. In each of these areas, and many more, Steve's strong stances influenced the thought of professional anthropologists as well as of general readers. As a result, paleoanthropology today, and indeed anthropology in general, would be very different places without him. What's more, even a decade after his premature death, Steve continues to provoke controversy among biological anthropologists. In his book *The Mismeasure of Man*, Steve excoriated the early nineteenth century craniologist Samuel Morton as an example of science in the service of unconscious prejudice: something against which he warned scientists should always be on guard. Now Steve himself has been accused of something similar in his attack on

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Morton; and the ongoing furor should help keep the current generation of biological anthropologists on their intellectual toes.

By the time I arrived at the American Museum of Natural History in 1971, as a very junior curator, Stephen Jay Gould had already flown the graduate coop and was comfortably ensconced at Harvard. I consequently never knew Steve quite as well as some of the other participants in this memorial symposium did, although I knew him for many years and greatly valued our acquaintanceship. My first opportunity to meet him other than formally thus came only in 1974, when we were both invited by the Wenner-Gren Foundation to attend a meeting on the *Phylogeny of the Primates: An Interdisciplinary Approach.*

Steve was, of course, anything but a primate specialist. But even at this early stage in his career, the reach of his writings had broadened well beyond the realms of invertebrate paleontology and evolutionary theory. Far enough beyond them, indeed, to mandate his inclusion in this highly specialized primate conference. Specifically, his remit was to cover two areas. One of these was evolutionary rates, a task he rejected—on the very unusual grounds, for him—that he had already said what he had to say on the issue. The second assignment was to cover the roles of ontogeny and neoteny in human evolution, a subject on which he published an important paper in *Science* with his colleague David Pilbeam later in the same year (Pilbeam and Gould 1974).

The Pilbeam and Gould size and scaling paper was very influential, less for its specific conclusions (simply stated in its own summary as: "*Homo sapiens* is a peculiar large primate; however, australopithecines are all versions of 'the same' animal"), than for re-animating studies of neoteny and heterochrony in human evolution, a vigorous area of research that has flourished ever since. The canonical work in this subfield remains Steve's first book, *Ontogeny and Phylogeny*, published three years later (Gould 1977a). But what I personally found most interesting at this early time was Steve's preprint for the conference (Gould 1974a). This contained, among much else, a virtuoso canter through the history of human evolutionary studies. In it Steve, at the beginning of his career, effortlessly displayed a mastery of a huge literature on a scale that many professional paleoanthropologists fail to achieve in entire academic lifetimes.

The meeting itself was held at Burg Wartenstein, the Wenner-Gren Foundation's historic conference center atop a mountain near Gloggnitz, in the foothills of the Austrian Alps. There we were comfortably incarcerated for a week with a dozen other colleagues, spending long periods around a large conference table that was fortunately adjacent to a well-stocked bar. But my interactions with Steve turned out to be less at the bar than over the ping-pong table, where we were encouraged to expend our animal spirits in place of disappearing on hikes out into the surrounding forests. Steve turned out to be as indefatigable and motivated at table-tennis as he was at the typewriter. I found playing against him every bit as exhausting as I did simultaneously arguing with him about the minutiae of paleoanthropology, and I caught more than a glimpse of the extraordinary inner energy that carried Steve not only through his incredibly voluminous writing, but through every other pursuit he undertook.

This brings me, in a very roundabout way, to Steve's intellectual legacy to anthropology. And, as so often with Steve, it is rather hard to know where to begin. For one thing, the sheer quantity of his writing, on anthropological topics as on all others he touched, is daunting. Thus, when I was invited to participate in this memorial conference, the first thing I did was what I suspect many of us did: namely, to head for my reprint cabinets, in search of my Gould, S. J. file. And while I remembered that file as a fat one, I must confess I was a bit taken aback to find not just one, or even two fat files, but six! The mere task of categorizing these voluminous writings wasn't easy, not least because, while he always carefully returned to his chosen subject, Steve regularly allowed himself to be carried away on any tangent that he found interesting. This elusive habit of discursiveness was, indeed, one of the features that made his innumerable *Natural History* columns so popular, and so addictive.

The hard-to-pin-down quality of much of Steve's writing is certainly what Michael Shermer encountered when, shortly after Steve's decease, he attempted to quantify the variety of his output, in an article in *Skeptic Magazine* subtitled: "Stephen Jay Gould as Historian of Science, and Scientific Historian" (Shermer 2002). Shermer felt strongly that Steve's success in popular writing had, in the eyes of many scientific colleagues, diminished the importance of his work due to what he called a "Sagan effect," whereby "one's popularity and celebrity with the general public was thought to be inversely proportional to the quantity and quality of real science being done" (Shermer 2002, p. 36). So, with an eye to restoring Steve's strictly scientific reputation as well as to documenting the sheer breadth of his output, Shermer undertook a quantitative analysis of Steve's 22 books, 101 book reviews, 479 scientific papers, and 300 *Natural History* essays "in terms of their subjects and themes."

Of course, merely by themselves these raw numbers demonstrate that, by any reasonable standards, Steve's peer-reviewed scientific oeuvre was hardly harmed by the volume of his popular works. But Shermer also pointed out how, even in terms of strictly scientific production, Steve's output is hard to classify. So elusive did he find it, indeed, that in the end Shermer came up with two alternative ways of quantifying Steve's scientific bibliography. The first approach was "minimal," placing the 479 technical papers in a mere five broad categories that are relatively easy to distinguish one from another, although obviously evolutionary theory and paleontology are quite closely entangled. And at this broad analytical level paleoanthropology, or even anthropology more generally, turned out not to be important enough categories to warrant notice. On the other hand, "paleoanthropology" *was* sufficiently important to figure in Shermer's alternative "maximal" classification, in which he recognized many more fields. Yet, even then, he could classify under this rubric only some 13 out of 479 publications, or well under 3 %, making it clear that Steve rather rarely ventured into the formal anthropological literature.

But what is equally clear is that pure quantitations of this kind entirely fail to reflect what is truly important. Namely, *impact*. And, despite a paucity of strictly technical contributions, there can be no doubt that Steve's influence on anthropology, and on paleoanthropology in particular, was truly seminal. In part, this influence was due to his many theoretically important contributions to the field of evolutionary biology to which paleoanthropology in part belongs. Foremost among such influences was obviously Steve's collaboration with Niles Eldredge (Eldredge and Gould 1972) in developing and publicizing the notion of "punctuated equilibria" that enabled paleoanthropologists, like other paleontologists, to treat the famous "gaps" in the fossil record as actual information.

This was truly important to the study of human evolution because, back in the early 1970s when Steve began to influence their field, paleoanthropologists were in thrall to a particularly fundamentalist notion of phyletic gradualism. And the Eldredge/Gould reformulation of evolutionary process gave some of us, at least, the theoretical ammunition necessary to begin throwing off those intellectual shackles. Similarly, it was Steve who, in collaboration with Elisabeth Vrba (Gould and Vrba 1982), insisted that *ex*aptation was a sufficiently important factor in evolution to deserve a name untainted by orthogenetic associations (as, for example, the popular term "preadaptation" was). And it has turned out that the exercise of clarifying this concept has forced us to recognize exaptation as an essential theme in the history of innovation in the human clade (see Tattersall 2012).

But in terms of specifics, I am convinced that Steve's most seminal contribution to paleoanthropology was his insistence from very early on that, as a consequence of its punctuated pattern, the genealogy of human evolution took the form of a bush with many branches, rather than a ladder (Gould 1975c,1976b). As I just briefly mentioned, during the two decades following 1950 the theoretical underpinnings for the study of the human fossil record were provided, at least in the Anglophone world, by what Steve characterized as a "hardened" version of the Evolutionary Synthesis (Tattersall 1995). Before World War II, paleoanthropologists had overwhelmingly been human anatomists by training, with little interest in patterns of diversity in the wider living world, or indeed in evolutionary mechanism. So, having been trained largely in a theoretical vacuum (and evidently feeling it), the postwar generation of paleoanthropologists was already exapted to capitulate when, at exact midcentury, Ernst Mayr told them to throw away nearly all the many names they had been using for fossil hominids (Mayr 1950). Mayr replaced this plethora, and the diversity it had suggested, by the idea that *all* fossil hominids known could be placed in a single time-transgressive succession:

*Homo transvaalensis* → *Homo erectus* → *Homo sapiens*

There was admittedly a certain degree of elegance in this new linear formulation; but the problem was that, even in 1950, it was not actually supported by the material evidence (see Tattersall 2009). Mayr's brashly reductionist vision of human phylogeny was, in reality, hugely incomplete.

New discoveries soon made not only most paleoanthropologists but even Mayr himself concede (grudgingly, in a footnote: Mayr 1953) that at least one small side-branch, the so-called "robust" australopiths, had indeed existed over the course of human evolution. But even so, right up into the 1970s and beyond, the minimalist mindset lingered; and, certainly in the English-speaking world, published human phylogenies remained resolutely linear. Steve's was among the first voices eventually raised to make paleoanthropologists aware that there was an alternative, and it was certainly the most widely influential.

In one of his early *Natural History Magazine* columns, Steve declared that he wanted:

> to argue that *Australopithecus*, as we know it, is not the ancestor of *Homo*; and that, in any case, 'ladders' [evolution as a continuous sequence of ancestors and descendants] do not represent the path of evolution (Gould 1976b, p. 26).

At the time, both statements flatly contradicted received wisdom in paleoanthropology. And while, in making the first of them, I suspect that Steve was rejecting *Australopithecus* as ancestral to *Homo* as a matter of principle as well as remembering his joint 1974 conclusion with David Pilbeam, his immediate rationale was based on the recent discovery in eastern Africa of specimens attributed to *Homo habilis* that were just as old as the South African australopiths. In hindsight, it is easy to quibble about Steve's use of the actual paleontological evidence for sidelining *Australopithecus*. But even at the time, his argument for the second assertion was compelling. Specifically in the context of the hominid fossil record, Steve wrote:

> The 'sudden' appearance of species in the fossil record and our failure to note subsequent evolutionary change within them is the proper prediction of evolutionary theory… Evolution usually proceeds by speciation… not by slow and steady transformation… repeated episodes of speciation produce a bush (Gould 1976b, p. 30).

Now of course, none of this was news to anyone who had read the 1972 Eldredge and Gould paper on punctuated equilibria. But it went against everything that paleoanthropologists had been taught for years to believe. And if, despite their inherited predilections, they were ready by now at least to lend Steve half an ear, it was because Steve himself had primed them to do so by his highly effective use of metaphor.

For Steve was a master of metaphor, which spun from his pen in an unending flow. Perhaps the most powerful Gouldian metaphors were architectural, such as his characterization (in collaboration with Dick Lewontin), of evolutionary byproducts as "spandrels"—incidentally, with special mention of the spandrels of San Marco in Venice (Gould and Lewontin 1979). But in paleoanthropology the "bushes versus ladders" image, first used in 1976, turned out to equally compelling. And it helped spur paleoanthropologists toward the realization that diversity was a fact of human evolutionary life that needed to be embraced, rather than denied. What's more, later discoveries in the field made it abundantly evident that Steve had been hugely prescient. For, as the human fossil record has grown by leaps and bounds over the last quarter of the twentieth century, it has become glaringly obvious how counterproductive the principled denial of diversity within it had been.

To provide some perspective here: In 1950, Mayr had recognized a mere three hominid species. By 1993, I was able to publish a hominid genealogy containing twelve. And the latest iteration of that tree embraces twenty-five species, in numerous co-existing lineages. This was exactly what Steve had predicted. In his 1976 article he had written:

> We [now] know about three coexisting branches of the human bush. I will be surprised if twice as many more are not discovered before the end of the century (Gould 1976b, p. 31).

Steve's influence, both as a wide-ranging evolutionary thinker and as author of an ongoing series of *Natural History* articles over the years, was thus a critical factor in preparing paleoanthropologists for the notion that the human evolutionary pattern had been not linear, but a matter of multiple branchings and evolutionary experimentations. Indeed, his impact on the paleoanthropological mindset went beyond even this, largely via his ceaseless insistence that human beings have not been an exception to general evolutionary rules. Before Steve's remonstrations began, one frequently heard the term "hominization" bandied around, as if becoming human had involved some kind of special process that was unique to our kind. And Steve's second great gift to paleoanthropology was to hammer home the message, with great eloquence and force, that human evolutionary history was just like that of other mammals, and that we should not be looking at human evolution as a special case of anything.

Of course, Steve had ideas on particular issues in human paleontology as well, and he never shrank from using his *Natural History* bully pulpit to voice his opinions on any paleoanthropological matters that caught his attention. Over the years he issued a succession of shrewd and often influential judgments on subjects as diverse as the importance of bipedality as the founding hominid adaptation (e.g. Gould 1975c, 1979b); the newly-mooted African "mitochondrial Eve" (e.g. Gould 1992); hominid diversity and the ethical dilemmas that might be posed by discovering an *Australopithecus* alive today (Gould 1997); sociobiology and evolutionary psychology (he did not like them: Gould 1976c, 1977b); the relations between brain size and intelligence (Gould 1974b); neoteny and the retention of juvenile growth rates into later development as an explanation of the unusual human cranial form (an issue discussed in detail in other contributions to this Symposium); and why human infants are so unusually helpless (Gould 1976a). But without doubt, Steve caused the most prolonged paleoanthropological uproar through his espousal of an issue of historical detail: his curious idea that the perpetrator of the Piltdown hoax was the French Jesuit priest, mystic and paleontologist Pierre Teilhard de Chardin.

As readers doubtless recall, during the four decades following 1912 British paleoanthropologists energetically promoted fossils collected at the site of Piltdown, in southern England, as those of the progenitor of the human lineage (see Spencer 1990). Put together, the Piltdown fragments produced a skull combining a curiously modern-looking cranium with an ape-like jaw. Eventually it was shown

(Weiner et al. 1953) that the artfully broken skull pieces fraudulently formed a composite skull, with cranial pieces from a modern human matched with a suitably modified fragment of orangutan jaw. These bones, and others, had been deliberately planted at the site; and, once revealed, the hoax became a huge embarrassment to paleoanthropology in general, and to British paleoanthropology in particular.

Immediately, of course, the search was on for the fraudster, and suspicion has at one time or another fallen on practically everyone possible, including the novelist Sir Arthur Conan Doyle, creator of the immortal Sherlock Holmes. Still, a hundred years after it was committed, the perpetrator of the fraud has yet to be identified definitively, though Charles Dawson, a local lawyer, was almost certainly involved somehow. It was Dawson who reported the first fossils from the Piltdown site, and he had not only the necessary knowledge, but also the opportunity and the access to the materials necessary to carry out the hoax. But Steve's minority pick was Teilhard de Chardin. Steve first wrote about Piltdown in a *Natural History* column published in 1979 (Gould 1979a); and although at this point he presented the affair as an enduring mystery, Teilhard was at front and center in his list of suspects. This outraged a lot of the radical cleric's admirers, and Steve found himself obliged to vigorously defend his interpretation. But Steve loved nothing more than a good fight, and the opposition encountered by his early ruminations clearly helped him crystallize his ideas about an episode that had fascinated him since boyhood. So, by the following year, he was ready to declare outright in the pages of *Natural History* that, in collusion with Dawson, Teilhard had beyond any reasonable doubt been the hoaxer (Gould 1980a).

Well, to cut a rather long story short (according to one of his editors, he ultimately wrote more words in *Natural History* about Piltdown than about any other individual subject: R. Milner, pers. comm.), Steve very effectively managed to reopen the dossier on this remarkable episode, and a spirited debate has sporadically raged since on the matter. But while the verdict on the identity of the hoaxer still remains open, Teilhard continues to be a very long shot indeed. Nonetheless, Steve's long dalliance with Piltdown gives us a dramatic manifestation of his fascination with history, in anthropology as much as in evolutionary science more generally.

Steve's devotion to the historically odd and curious, as well as with the mainstream development of scientific ideas, is also well illustrated by his detailed account of the bizarre nineteenth-century story of Saartjie Baartman (Gould 1982, 1985). Saartjie, dubbed the "Hottentot Venus" was a Khoisan woman from South Africa's Western Cape region who was brought to Europe in 1810 and widely exhibited to the public before her death in 1815. Steve's publicizing of the extraordinary events surrounding and following Saartjie's exhibition may or may not have contributed to the repatriation in 2002 of her remains from Paris to South Africa, where they now rest on a hilltop overlooking the valley in which she was born. But what is certain is that Steve's interest in this sad case also reflected another of his long-term concerns, namely with what he called "scientific racism."

Indeed, it seems fair to say that Steve's concern with the tragic history of Western racism was the aspect of his interests that intersected most deeply with those areas of anthropology lying beyond strict human evolutionary studies. He even made the matter personal, with a lucid and deeply thoughtful demolition in *Natural History* of the purportedly scientific bases for discrimination against Jewish immigrants to America furnished by such savants as H. H. Goddard and Karl Pearson (Gould 1980b). By this point, and principally in the 1970s—when memories of the struggle during the previous decade for civil rights in the United States were still extremely raw—Steve had already devoted a long series of columns in *Natural History* magazine to the subject of racism, as it presented itself in a whole host of different guises. In his very first year of writing for *Natural History*, he ruminated on the "race problem" both as a taxonomic issue (Gould 1974d), and in its more political expression in relation to intelligence (Gould 1974c). He also began his long-lasting and more specific campaign against genetic determinism, via a broadside (Gould 1974b) against the conclusions of Arthur Jensen, the psychologist who had argued that education could not compensate for the allegedly different performances of various ethnic groups on IQ tests. And he shortly thereafter began a vigorous and still somewhat controversial exploration of the historical roots of "scientific racism" in the work of nineteenth-century embryologists such as Ernst Haeckel and Louis Bolk (e.g. Gould 1975a), bringing into the story once again his longstanding interest in neoteny and developmental trajectories.

But Steve's most widely-noticed and best-publicized contribution to the race issue began in 1978, with his attack on the conclusions of the early nineteenth-century physician and craniologist Samuel George Morton, whom he characterized rather snarkily as a "self-styled objective empiricist" (Gould 1978, p. 503). In a voluminous work titled *Crania Americana*, published in Philadelphia in 1839, the widely-admired Morton had presented the results of the most extensive study ever undertaken of human skulls. The main thrust of this study had been to investigate the then intensely-debated question of whether the various races of human kind had a single origin, or had been separately created. Morton opted for polygeny, the multiple origin: a conclusion that was hardly guaranteed to endear him to Steve. And, along the way, Morton presented measurements that showed, in keeping with prevailing European and white American beliefs of racial superiority, that whites had larger brains than native Americans, who in turn had bigger brains than blacks did.

But, after closely examining Morton's data, Steve peremptorily characterized the Philadelphia savant's conclusions as:

> a patchwork of assumption and finagling, controlled, probably, by his conventional a priori ranking (his folks on top, slaves on the bottom) (Gould 1978, p. 504).

He excoriated Morton for a catalogue of sins that included inconsistencies of criteria, omissions of both procedural and convenient kinds, slips and errors, and miscalculations. And although in the end he found "no indication of fraud or conscious manipulation" (Gould 1978, p. 509), he did see "Morton's saga" as "an… egregious example of a common problem in scientific work" (p. 509). As scientists we are all, Steve asserted, unconscious victims of our preconceptions, and the "only palliations I know of are vigilance and scrutiny" (p. 509). This blanket condemnation of past and current scientific practice, based on his reading of the work of a Philadelphia physician who had died a hundred and thirty years earlier, was a theme Steve shortly returned to, with a vengeance, in his bulky volume *The Mismeasure of Man* (Gould 1981). Probably no book Steve ever wrote commanded wider attention than did this energetic critique of the statistical methods that had been used to substantiate one of his great *bêtes noires*, biological determinism. This was the belief that:

> the social and economic differences between human groups—primarily, races, classes, and sexes—arise from inherited, inborn distinctions and that society, in this sense, is an accurate reflection of biology" (Gould 1981, p. 52).

Steve inveighed energetically against this attitude, and at every opportunity, throughout his career. And in *Mismeasure*, as in his *Science* paper, he made no effort to hide his belief that statistical methods had routinely been abused in the service of cultural preconceptions.

In *Mismeasure*, Steve restated his case against Morton at length, adding to the mix a robust rebuttal of methods of psychological testing that aimed at quantifying "intelligence" as a unitary attribute. One of his prime targets was inevitably Arthur Jensen, the psychologist he had already excoriated in the pages of *Natural History* for his famous conclusion (Jensen 1969) that the "Head Start" programs, designed to improve the performance of poorly-performing African–American schoolchildren, were doomed to fail because the hereditary component of their performance was hugely dominant over the environmental one. A predictable furor followed the publication of *Mismeasure*, paving the way for continuing controversy during the 1980s and 1990s on the question of the roles of nature versus nurture in the determination of intelligence.

This issue of nature versus nurture, a choice between polar contrasts, is of course designed for polemic, and most attempts to find a more nuanced middle ground are usually drowned out by the extremes. So it was in Steve's case. As an unrepentant political liberal he was, of course, firmly on the side of nurture, and he brooked no compromise on the matter. And as a result of his uncompromising characterizations of his opponents' viewpoints, Steve found himself frequently accused by Jensen and others of misrepresenting their positions, and of erecting straw men to attack.

Yet even after *Mismeasure* appeared, the climax of the debate was yet to come. The book's first edition of appeared in 1981, long before Richard Herrnstein and Charles Murray published their notorious volume *The Bell Curve: Intelligence and Class Structure in American Life*, in 1994. At positively Gouldian length, Herrnstein and Murray gave a new boost to the argument that intelligence is largely inherited, proclaiming that innate intelligence was a better predictor of such things as income, job performance, chances of unwanted pregnancy, and involvement in crime, than are factors like education level or parental socioeconomic status. They also asserted that, in America, a highly intelligent "cognitive elite" was becoming separated from the less intelligent underperforming classes, and in consequence they recommended policies such as the elimination of what they saw as welfare incentives for poor women to have children.

To Steve Gould, the premier public denouncer of racism, such claims were like a red rag to a bull. And, as a longstanding excoriator of such evils as biological determinism, eugenics, scientific racism and sociobiology, as well as in his role as steadfast champion of social equality, Steve led the charge against Herrnstein and Murray's views. Hard upon the publication of *The Bell Curve*, he published a long *New Yorker* article (Gould 1994) attacking the four unsubstantiated assertions on which he claimed Herrnstein and Murray's argument depended. In order to be true, Steve said, Herrnstein and Murray's claims required that what they were measuring as intelligence must (1) be representable as a single number; (2) allow linear rank ordering of people; (3) be primarily heritable; and (4) be essentially immutable. None of these assumptions, he declared, was tenable. And two years later (Gould 1996) he returned to the attack with a revised and expanded edition of *Mismeasure* that took direct aim at Herrnstein and Murray's long book.

There can be little doubt that, as articulated in both editions of *Mismeasure*, Steve's conclusions found wide acceptance not only among anthropologists but in the broader social arena as well. But at the same time it is necessary to note that doubts have lingered about Steve's broad-brush approach to the issues involved, and particularly about a penchant he had to neglect any nuance there might have been in his opponents' positions. This particular leaning meant that, as significant as Steve undoubtedly was as an historian of science, he was capable on occasion of writing Whiggish history. Indeed, it has turned out that he was capable of committing in his own writings exactly the kind of error of which he had accused Samuel Morton. Ironically, even in the very case of Morton himself.

In June 2011, a group of physical anthropologists led by Jason Lewis published an exegesis of Steve's attacks on Morton's craniology in *Science* and in the two editions of *Mismeasure.* Steve's allegations that Morton had manipulated (or at least selected) his primary data "to fit his preconceptions about human variation" (Lewis et al. 2011, p. 1) had, these authors suggested, effectively destroyed the formerly-esteemed Morton's posthumous reputation. But by re-measuring the cranial capacity of about half of Morton's extensive sample of human skulls, Lewis and colleagues discovered that the data reported by Morton had on the whole been pretty accurate. They could find no basis in the specimens themselves for Steve's suggestion that Morton had (albeit unconsciously) over-measured European crania, and under-measured African or Native American ones. What's more, they could find no evidence that, as alleged by Steve, Morton had selectively reported his samples. Or that he had attempted to lower the observed mean in American Indian brain size. Or had used sexual size differences to skew his results. Or had systematically repeated any erroneously reported means.

The anthropologists did concede that Morton had attributed various psychological characteristics to different racial groups. But they pointed out that, while Morton was inevitably a creature of his own times, he had done nothing to dissimulate his racial prejudices or his polygenist sympathies. And they concluded that, certainly by prevailing standards, Morton's presentation of his basic data had actually been pretty unbiased. What is more, while they *were* able to substantiate Steve's claim that Morton's final summary table of his results contained a long list of errors, Lewis and colleagues also noted that those errors were not of a kind that would have materially affected his conclusions. Indeed they found, to the contrary, that correcting those errors would actually have served to reinforce Morton's own declared biases. And they even discovered that Steve had reported erroneous figures of his own.

All in all, Morton emerges from this re-analysis as more sinned against than sinning. And it is hard to refute the authors' conclusion that Steve himself had been prepared to allow his own unconscious biases to color his judgment of this early nineteenth-century scientist. Morton naturally enough carried all of the cultural baggage of his time, ethnicity, and class. But so, it seems, did Steve. And the biggest irony in this whole affair is that, as I told the *New York Times* after Lewis and colleagues published their analysis, in a paradoxical way Steve had proved his own point. Scientists are indeed human beings, and when analyzing evidence they always have to be on guard against the effects of their own personal predilections. But it is perhaps almost inevitable that, on occasion, even the most vigorous guard will slip.

The resulting errors will usually concern matters of detail, as seems to have been the case with the mistakes of which Steve accused Morton. But Steve himself was never a detail man, certainly as concerned anthropology. His great strength always lay in the big picture. Equally significantly, at the point where science and society intersect—as is routine in anthropology, rather than the exception, as in most other areas of science—Steve brooked no compromise. He was an egalitarian polemicist, who saw matters of principle in black-and-white; and this made it inevitable that he would disregard the occasional nuance.

Still, in the end these larger-than-life Gouldian traits are trivial in the context of Steve's greater intellectual legacy to anthropology. For one thing, while this legacy is both seminal and significant, it is also indirect. It does not concern specialist matters. And neither should it. Steve was a fossil snail expert and an evolutionary macrotheorist, not an anthropologist. And his influence in the tangential field of anthropology correspondingly involved metaphor and mindset rather than bricks and mortar.

Perhaps most importantly, Steve's tireless propagation of the bush-versus-ladder imagery influenced the perspective of an entire generation of paleoanthropologists, just as it did their brethren in other areas of evolutionary biology. And it is not hard to discern how, over the years, Steve's admonitions helped produce significant changes in the way in which paleoanthropologists looked at the fossil record they studied. Among human biologists the influence of Steve's insistence on the equality of potential among the races of humankind was equally pervasive. There is no doubt whatever that Steve's humane and passionate writing in defense of racial equality will be looked upon by future anthropologists and historians as a beacon of rational positivism in an age in which genetic reductionism was showing alarming signs of resurgence—as indeed it still is, as race-stratified genome-wide association studies continue to dominate research on human variation (see Tattersall and DeSalle 2011; Barbujani 2013).

And it is this issue of scale, I think, that provides us with the appropriate perspective from which to view the Morton affair. As Steve's longtime friend, the anthropologist Richard Milner, told a correspondent from *Discover* magazine:

> If [Steve] went off on a mistaken path, as he sometimes did, any question of deliberate fraud or hoax is absolutely out of the question. Whatever conclusions he reached on an issue, rightly or wrongly, he did with complete conviction and integrity… Steve was a tireless combatant against racism in any form. If he was guilty of the kind of unconscious bias in science that he warned against, at least his bias was on the side of the angels (quoted in Saletan 2012, p. 67).

Amen to that.

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# Mismeasuring Man Thirty Years Later

**Guido Barbujani**

**Abstract** Humankind has long been regarded as naturally divided into distinct groups or races, much like other animal species. Only in the second half of the twentieth century, through the work of Frank Livingstone, Richard Lewontin and Stephen Jay Gould, the race concept began to be questioned as a useful tool for understanding human biodiversity. Recent genomic studies have shown that we are all different, and that there are geographical patterns in human genetic variation. However, these patterns do not allow one to define clusters of biologically differentiated individuals, because each human population harbors a large share of the species' genetic diversity, and each individual genome is a mosaic of DNA fragments of different origins. These data explain why studies of human morphology never led to an agreement about the number and definition of human races, with proposed races numbering from 2 to 200; people can be clustered in many ways, but variation within clusters is always large, and most alleles are cosmopolitan, i.e. present, at variable frequencies, in all continents. Race remains an important component of our social and psychological world, but envisaging our species as subdivided in genetically-differentiated groups leads to poor evolutionary inference and to errors in clinical practice.

## 1 Against Biological Determinism

Gould's (1981) *The mismeasure of man* is a powerful confutation of biological determinism, i.e. the idea that what we are and can possibly be is written in our genes. In 1994, biological determinism would reach its most radical modern expression with the best seller *The bell curve*. In that book, Herrnstein and Murray

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(1994), respectively a psychologist and a political scientist, claimed that intelligence is accurately measured by the Intelligence Quotient (IQ); that the IQ is genetically determined, constant through life, and basically unaffected by social or economical factors; and that a “cognitive elite” of biologically gifted people is endangered by the US social policies, transferring resources from the rich (and therefore intelligent) to the poor, and thus favoring a higher fertility of biologically inferior people. Whatever one might think of the political aspects of Herrnstein and Murray’s proposal, the biological flaws of their book would have been less phenomenal, had they paid any attention to *The mismeasure of man*. Throughout seven dense and beautifully written chapters, Gould showed that no scientific evidence suggests that the social and economic differences between human groups—primarily races, classes and sexes—arise from inherited, inborn differences, and so the social stratification is by no means an inevitable reflection of biological hierarchies.

Mismeasuring man, in Gould’s view, means that the methods developed to describe and make sense of human biological diversity are often misused to dissolve individuals into arbitrary racial categories, which are there ranked based on pseudoscientific criteria. A convincing illustration of this process is in a later book, *I have landed* (Gould 2011). In 1836, the German anatomist Tiedemann published a study *On the Brain of the Negro, compared with that of the European and the Orang-Outang*. The title is misleading; actually, Tiedemann believed in human equality; his intention was not to suggest a close relationship between African humans and Asian apes, but to scientifically investigate what was then a hot topic, variation in human brain size. In that paper, appeared on the pages of a prestigious scientific journal, the *Philosophical Transactions of the Royal Society of London*, Tiedemann measured the internal size of 200 human skulls and estimated the respective cerebral masses. On average, the Caucasians’ brains (weighing more than 40 oz) were heavier than those of the other four groups compared, namely the Malay (39.84), the Americans (39.33), the Mongols (38.94) and the Ethiopians (37.84). Some of these terms have a different meaning today, but in the nineteenth century they were rather obvious to most scientists. Indeed, they referred to the race classification system proposed by J.F. Blumenbach, who, besides inventing the term Caucasian (soon to become synonymous with white-skinned people), called Malay the Australians, Mongols the Eastern Asians, and Ethiopians the Africans.

Blumenbach’s racial catalog was derived from Linnaeus’, who had started the scientific study of human diversity. In the 9th edition of his S*ystema naturae*, Linnaeus proposed a list of six races, one of them including carriers of congenital anomalies (*Homo sapiens monstruosus*), and another one hybrids between humans and other species whose existence has not been confirmed by later work (*Homo sapiens ferus*). The remaining four races (*europaeus, luridus, afer, americanus*) corresponded to four continents (Oceania was missing) but also to the four elements of classical Greek philosophy, namely air, water, earth, and fire. Races were thus defined by a combination of physical and psychological traits, so that the Americans were described as choleric, the Europeans sanguine, the Asians melancholic, and the Africans phlegmatic. Some of the most prominent naturalists of the nineteenth century, Buffon and Cuvier among them, modified Linnaeus' taxonomy, splitting or collapsing some of the previously proposed races (Cohen 1991). Like Tiedemann, and unlike several anthropologists of their time who attributed Europeans, Africans and Asians to distinct species, Blumenbach was a firm believer in the unity of humankind. However, he also felt that the existing human diversity was caused by a process of degeneration from an original, ideal human form, presumably caused by some kind of reaction to climate. In his opinion, the people from the Caucasus were the most beautiful on Earth; following an aesthetic criterion he chose them as a paradigm of native, undegenerated humankind. Because the degeneration he had in mind occurred in two directions, he needed two intermediate races separating the Caucasians on the one hand from the Mongols and the Ethiopians on the other. By adding to Linnaeus' races a fifth group, the Malay or Australians, Blumenbach envisaged the evolution of human diversity as a process whereby the Caucasians had given rise to Americans and Malay, in the process ultimately leading to Ethiopians and Mongols.

Blumenbach's thesis was intriguing (and wrong), but when it was published there were simply no data to test it. Tiedemann's study appeared to support it, suggesting a distribution of average brain sizes consistent with Blumenbach's expectations. In his 2011 essay, Gould reconsidered the whole skull dataset, showing that differences between members of the same group were much larger than those between the group averages; in other words, brain sizes of people from all continents overlapped, ranging from small to large, with many intermediate values. The greater variation between individuals of the same group than between group averages, in remarkable agreement with what was later observed for scores of human traits, means that group averages are poorly informative. But, in this as well as in other cases, only part of the scientific message got through. Despite both Blumenbach and Tiedemann stating that in the appropriate environment any human could be capable of the most sophisticated levels of artistic expression, average brain sizes were long considered as a good approximation to a measure of the groups' intelligence. Tiedemann analysis of human diversity was thus used to rank groups of people, and the undemonstrated assumption that the ranking reflected objective biological factors became, for many, a fact. Once more, mismeasuring man had resulted in increased ignorance and prejudice.

## 2 Compiling the Catalog of Human Races

Both race and prejudice have a long story. As for the former, for centuries people sharing the same 'blood', especially in noble families, were said to form a race (Cohen 1991). In the eighteenth and nineteenth centuries, the word came to designate constant human types, and it was used both to describe and to explain human diversity. Naturalists classified people in different races, and explained their differences as a consequence of their belonging to different races.

## *2.1 Species are Ambiguous, Races Even More*

However, almost in the same years, the race concept was also becoming intrinsically ambiguous. For creationists such as Linnaeus, species were fixed entities; there were no conceptual difficulties in assigning individuals to species, and also to subdivisions of lower taxonomical rank. The ambiguity arose when the very concept of species was called into question by Lamarck and Darwin. Indeed, if different species arise with modification from common ancestors, the borders between them exist only from a certain moment on. In modern terms, a species is a group of organisms capable of interbreeding and producing fertile offspring, reproductively isolated from other such groups (de Queiroz 2005). As a consequence, a race or subspecies is a genetically differentiated group of organisms on its way to developing reproductive isolation from other groups of the same species, but not there yet; this way, its borders are uncertain, and so is the attribution of individuals to any such group. Aware of that difficulty, Mayr (1947) stressed that in some species populations with different character combinations are separated by borders, whereas in other species biological changes are gradual and continuous; only in the former it makes sense to speak of subspecies or geographic races. Many authors of human genetics (for example Vogel and Motulsky 1986) and anthropological (Brues 1977; Molnar 1998) textbooks essentially borrowed this definition, with a significant difference—they took for granted that there are indeed biological borders among human groups. Races were then defined as sets of individuals who share a significant fraction of their genes because of shared ancestry, and can be distinguished from other races by their common gene pool. Compiling the list of human races was then the biological anthropologists' main task.

It was not only Vogel and Motulsky (1986), Brues (1977) and Molnar (1986) who avoided addressing the question whether human diversity is really discontinuous. The idea that humans are naturally divided in clusters of genealogically-related individuals, and hence that a scientific study of humans starts from their racial classification, was long unchallenged (Cohen 1991). People differ in many aspects, from facial traits, to height, weight, body structure, skin and hair color; often these differences allow one to guess with some accuracy a person's geographical origin. The classical, typological, approach consists then in defining some basic human types on the basis of such traits, and then attributing each individual to one of those types, or races. Ideally, most individuals should fall unambiguously into the appropriate group, except perhaps for a minority of them, which would be regarded as derived from interracial crosses. However, in the real world this view has two problems. The first is that there is an unavoidable degree of arbitrariness in the way we describe people. To mention just an example, the number of possible skin colors recognized by different authors has fluctuated between four and 34 (Cohen 1991). Also, because each culture gives special importance to different facial and bodily traits, the same individual may be described very differently by members of different communities (Foster and Sharp 2002; Pauker and Ambady 2009); to complicate matters even further, social status has been shown to affect the way people are classified in races (Weeks and Lupfer 2004). The second problem is that every human group contains various proportions of people who do not resemble much, or at all, the average individual, whatever that term might mean. It comes as no surprise, then, that the many proposed lists of human races have only one feature in common, namely that each of them contradicts all the others.

## 2.2 *Too Many Races, and Never the Same*

An incomplete selection of the racial catalogs developed under a typological approach is in Table 1; see also Cohen (1991) and Molnar (1998). It is interesting to note that the numbers of items featured in each catalog increased, at least until the second half of the twentieth century. As explorers explored, as travelers travelled, European and North American scientists came in contact with new

**Table 1** Some lists of proposed Human races

| Author | No. of races | Races proposed |
|---|---|---|
| Linnaeus (1735) | 6 | Europaeus, Luridus, Afer, Americanus, Ferus, Monstruosus |
| Buffon (1749) | 6 | Laplander, Tartar, South Asian, European, Ethiopian, American |
| Blumenbach (1795) | 5 | Caucasian, Mongolian, Ethiopian, American, Malay |
| Cuvier (1828) | 3 | Caucasoid, Negroid, Mongoloid |
| Deniker (1900) | 29 | |
| Weinert (1935) | 17 | |
| Von Eickstedt (1937) | 38 | |
| Coon et al. (1950) | 30 | |
| Biasutti (1959) | 53 | |
| Coon (1962) | 5 | Congoid, Capoid, Caucasoid, Mongoloid, Australoid |
| Garn (1961) | 9 | African, European, Asian, Indian, Amerind, Melanesian, Polynesian, Micronesian, Australian |
| US Census Bureau (2000) | 6 | White, Black or African-American, American Indian and Alaska Native, Asian, Native Hawaiian and other Pacific Islander, Hispanic or Latino |
| US Census Bureau (2010) | 15 | White, Black or African-American, American Indian and Alaska Native, Asian Indian, Chinese, Filipino, Japanese, Korean, Vietnamese, Other Asian, Native Hawaiian, Guamanian, Samoan, Other Pacific Islander, Hispanic or Latino |
| Risch et al. (2002) Fig. 1 | 5 | African, Caucasian, Pacific islanders, East Asian, Native American |
| Risch et al. (2002) Table 3 | 5 | African Americans, Caucasians, Hispanic Americans, East Asians, Native Americans |

Compiled from Cohen (1991), Madrigal and Barbujani (2006), Coon et al. (1950), Garn (1961), where the original references can be found populations, which proved difficult to fit into the existing races. Thus, new races had to be invented and the catalogs expanded. Lists compiled by serious scientists include anything between three and 200 different races (Barbujani 2005), and it is extremely challenging to identify in these lists anything that can be called "common concepts" of race. With growing numbers of races, their borders became first ambiguous, and then very ambiguous. In a recent article claiming that racial categorization is scientific and objective, Risch et al. (2002) used two different racial catalogs, apparently failing to notice it. When defining genetic clusters of individuals that would comply with traditional definitions of races became exceedingly difficult, there were attempts to categorize people by "self-reported ancestry" (Rosenberg et al. 2002) or "self-defined race" (Risch et al. 2002). However, resorting to folk definitions of race can only further increase the arbitrariness of the exercise. Three examples, among many: (1) Whereas in the USA both Japanese and Chinese people would be considered to be Asian, in apartheid South Africa the former were considered to be white and the latter colored; (2) In Japan, the majority of the population considers the ethnic group burakumin as biologically distinct from them, but in the USA both groups would be considered part of the same race; (3) The US Census Bureau asks residents to choose the race with which they most closely identify; the number of possible answers changed every decade, from 8 (1890) to 11 (1920), 9 (1930), 12 (1960), 6 (2000), and 15 (2010).

In time, all this inevitably led to question the usefulness of the race concept as a tool to describe human diversity. In an article entitled "On the nonexistence of human races", Frank Livingstone (1962) stressed that humans are doubtless biologically different from one another. However, he also observed that different genetic loci give discordant information on the individuals' relationships, that human genetic variation is distributed in continuous gradients over the geographical space, and that biological boundaries between human groups have been inconsistently defined through time. Not all scientists agreed, including Theodosius Dobzhansky (1973), who maintained that human biological diversity is properly described in terms of racial differences. Dobzhansky admitted that there was no consensus on the number and definition of human races, but was confident that future genetic studies would settle the issue. Recently, inconsistencies in racial classification were recognized, but not taken to invalidate the race concept, by authors such as Levin (2002) and Harpending (2007), whereas Brown and Armelagos (2001) and Relethford (2003) deemed scientifically unacceptable a classification system based on ill-defined categories.

## 3 Measuring Genetic Diversity

Contrary to Dobzhansky's predictions, the discussion on race is still heated, but he was right in predicting that abundant genetic evidence would become available. In the last decades, especially with the development of fast and efficient methods for studying large sections of the genome, genetic diversity has been thoroughly investigated in hundreds of human populations. Now we know that the (haploid) human genome size is about 3.2 thousand million nucleotides, with large differences between individuals due to copy-number variation (CNV), i.e. deletions, insertions, duplications and more complex rearrangements of the genome (Redon et al. 2006); some 36 million variable nucleotide sites are known (see http://browser.1000genomes.org/index.html) and their number is steadily increasing; the average nucleotide difference between humans and chimps is about 40/1000 (Varki and Altheide 2005), and between random members of our species about 1/1000 (Jorde et al. 2000). The percentages of the global species variance reported in the next section are fractions of the last mentioned figure.

Coming to differences between species, humans have the lowest levels of DNA diversity among primates. Individual variation in humans is half that observed in gorillas, and less than one third that observed in orangutans and chimpanzee (Kaessmann et al. 2001). Differences between populations are often summarized by Wright's $F_{ST}$, a statistic ranging from 0 when all populations are identical, to 1 when different alleles are fixed in the populations (see Barbujani and Colonna 2010), a condition never observed in humans so far (Pickrell et al. 2009; Xing et al. 2010). Differences between gorilla ($F_{ST} = 0.38$; Thalmann et al. 2007) and chimpanzee ($F_{ST} = 0.32$; The Chimpanzee Sequencing and Analysis Consortium 2005) populations are more than twice as high as between human populations ($F_{ST} \leq 0.15$). Thus, not only are individual differences in humans much smaller than between individuals of other primate species, but also these small differences are mainly accounted for by individual differences within populations. In other words, we are subdivided into more closely related populations than any of our evolutionary relatives (with the possible exception of bonobos, *Pan paniscus*), even though humans occupy much of the planet and other apes live in restricted geographic areas.

## *3.1 Early Studies*

It was Richard Lewontin (1972) who in the pre-DNA era pioneered the approach of breaking down the overall genetic diversity of the species in three hierarchical components. Under that approach, each individual is compared to all other individuals studied, and their genetic differences are counted. Three statistics are then estimated from those counts, namely the average variance: (a) between individuals of the same population; (b) between populations of the same group; (c) between groups. Lewontin (1972) analysed protein variation at 17 genetic loci, assuming a seven-race classification system; other authors chose the same (Latter 1980) or a three-race (Ryman et al. 1983) system. In all cases, individual differences between members of the same population accounted for some 85 % of the global human variance (Table 2), with values for individual loci ranging from 63.6 to 99.7 %. Belonging to different populations added between 3 and 8 % to that value, and

**Table 2** Estimated fractions of the global human diversity at three hierarchical levels of population subdivision

| Polymorphism, number of loci | Reference | Within population | Between populations, within race or continent | Between races or continents |
|---|---|---|---|---|
| Protein, 17 | Lewontin (1972) | 85.4 | 8.3 | 6.3 |
| Protein, 18 | Latter (1980) | 85.5 | 5.5 | 9.0 |
| Protein, 25 | Ryman et al. (1983) | 86.0 | 2.8 | 11.2 |
| Autosomal DNA, 109 | Barbujani et al. (1997) | 84.4 | 4.7 | 10.8 |
| Autosomal DNA, 90 | Jorde et al. (2000) | 84.8 | 1.6 | 13.6 |
| Autosomal DNA, 21 | Romualdi et al. (2002) | 82.9 | 8.2 | 8.9 |
| Autosomal DNA, 377 | Rosenberg et al. (2002)[b] | 93.2 | 2.5 | 4.3 |
| Autosomal DNA, 377 | Rosenberg et al. (2002)[c] | 94.1 | 2.4 | 3.6 |
| *Alu* insertions, 100 | Watkins et al. (2003) | 88.6 | 1.9 | 9.6 |
| X chromosome, 17 | Ramachandran et al. (2004) | 90.4 | 4.6 | 4.9 |
| Autosomal insertion/deletions, 40 | Bastos-Rodrigues et al. (2006) | 85.7 | 2.3 | 12.1 |
| Median, all loci | | 85.5 | 2.8 | 9.0 |
| Median, normalized[a] | | 87.9 | 2.9 | 9.2 |

[a] These values were obtained by considering all studies equally informative. The medians of their results at the three levels of population subdivision were normalized by dividing them by the total (97.3) and multiplying by 100

[b] Considering five groups: Africa, Eurasia, East Asia, Oceania, Americas

[c] Considering the seven groups obtained by further subdividing Eurasia into Europe, Middle East, Central/South Asia

belonging to different groups or races between 6 and 11 %. At the protein level, therefore, variation among putative races seemed to represent less than one tenth of our species' overall genetic diversity. Lewontin concluded his paper with a sentence that became famous and was the source of endless discussion: "Human racial classification is of no social value and is positively destructive of social and human relations. Since such racial classification is now seen to be of virtually no genetic or taxonomic significance either, no justification can be offered for its continuance".

## *3.2 Studies at the Genomic Level*

The proportions of variance estimated from protein data by Lewontin (1972), and confirmed by Latter (1980) and Ryman et al. (1983), appeared at first counterintuitive and were met with some degree of disbelief, but later DNA analyses confirmed them with remarkable precision. An impressive amount of data of human diversity, including at present more than 1000 complete genome sequences, accumulated in the last decade (see Clarke et al. 2012). Estimates of the proportion of genetic variance between populations inferred from up to 2,841,354 Single-Nucleotide Polymorphisms (SNPs) vary between 0.05 (Auton et al. 2009) and 0.12 (Xing et al. 2010), with most values close to 0.11 (reviewed in Barbujani and Colonna 2010). In practice, each human population harbors a large share of the genetic diversity of the whole species. If all humankind got extinct except for one population, we would expect to lose only about 11 % of the overall diversity of the species—actually, much less if the surviving population were African (Rosenberg et al. 2002). Another way to describe these results is to say that, if we arbitrarily set to 100 the maximum genetic difference between two humans, the expected difference between two members of the same community is about 89, i.e. much more than previously illustrated definitions of race appear to imply. All these figures were estimated from isolated populations of anthropological interest. Urban populations would be a more typical sample of humanity, and indeed a UN document released in 2008 reports that half of all humans live in urban areas. This means that the within-population component of genetic variance is underestimated in the available studies and that, if subjects were sampled at random all over the planet, differences between populations and groups thereof would account for an even smaller fraction of the species' variance.

The analysis of large genomic datasets is showing why it proved impossible to find an agreement on the main biological groups of humankind. Among nearly 250,000 polymorphic genome sites, no SNP was founds at which a fixed difference would distinguish any pair of continental populations (Xing et al. 2010). More than 80 % of human SNPs are cosmopolitan: that is, the two alleles occur, at different frequencies, in all continents (Table 3; Jakobsson et al. 2009). Combinations of alleles on the same chromosome, or haplotypes, have a clearer geographical distribution, but, with the exception of Africa, continent-specific haplotypes are a small proportion of the total haplotypes of the species (Table 3; Jakobsson et al. 2008). A similar pattern was found in the analysis of long DNA stretches, or haplotype blocks, in which two main classes of haplotypes were described, one exclusively African, including 26 % of the blocks, and the other worldwide distributed, including more than half of the blocks; very few blocks, less than 2 %, were found to be specifically restricted to Europe or Asia (Gabriel et al. 2002).

**Table 3** Percentage of continent-specific and cosmopolitan genetic variants inferred from the analysis of 525,910 SNPs and 396 CNV in 29 populations (Jakobsson et al. 2009)

| Polymorphism distribution | SNPs | Haplotypes | CNVs |
|---|---|---|---|
| Exclusively African | 0.91 | 18.03 | 5.10 |
| Exclusively Eurasian | 0.75 | 5.70 | 4.75 |
| Exclusively East Asian | 0.06 | 2.16 | 2.91 |
| Exclusively American | 0.05 | 1.40 | 5.73 |
| Exclusively Oceanian | 0.01 | 1.74 | 12.33 |
| Cosmopolitan | 81.17 | 12.43 | 61.19 |

The columns do not sum up to 100 because many variants are shared between 2, 3 and 4 continents

This means that, with limited exceptions, human genomes belong to two major groups, either specifically African or generically human. In addition, and in agreement with Livingstone's (1962) intuition, different sets of polymorphisms, and especially Copy Number Variants (CNVs) versus SNPs, show different geographic distributions, and hence would suggest contradictory subdivisions of individuals and populations (Table 3). It seems likely that these differences reflect, at least in part, different selective regimes affecting different genome sections (Novembre and Di Rienzo 2009). Finally, detailed analyses of individual chromosomes show that in general people's genomes are mosaics of DNA regions of different origins, brought together in the same individual by continuous processes of population admixture (Halder et al. 2009).

## 4 We are All Different, But How Different?

The genetic differences between populations, probably representing some 11 % of the global species variance, are small, but not zero. Analysis of inter-population differences shows that both allele frequencies and DNA sequences vary nonrandomly in space, often forming gradients over entire continents (Ramachandran et al. 2005; Liu et al. 2006). We also know that zones of sharp genetic change, or genetic boundaries, exist, and tend to overlap with various kinds of migrational barriers, both physical (e.g., mountain ranges or large bodies of water) and cultural (especially language boundaries) (Sokal et al. 1990). However, very seldom do genetic boundaries form complete rings around single populations or groups of populations. Virtually all populations studied are somewhat different from their neighbors, but continuous variation is the rule over much of the planet, with the genetic characteristics of the various regions changing smoothly in the geographical space (Jorde and Wooding 2004).

Based on these genetic differences, individuals can often be assigned to populations. By selecting polymorphisms among the most variable of the genome, Witherspoon et al. (2007) could correctly classify most people from different geographical origins. However, the error rate remained substantial even when individuals from different continents, such as sub-Saharan Africa and Europe, were compared. The accuracy of the assignment depends on the degree of differentiation between populations, on the number of populations being compared (the more, the higher the error) and on the number of polymorphisms considered (Romualdi et al. 2002; Witherspoon et al. 2007).

On the other hand, the genetic differences between populations are not zero, but are small. Once the analysis of highly variable polymorphisms has shown that a certain individual has a good probability of belonging to a certain population, predicting that individual's genotype at other loci is problematic, because different polymorphisms show different patterns of variation. Despite that difficulty, and although few statisticians would try to discriminate groups when the variance within them is 8–9 times as large as that between them, identifying even moderately differentiated genetic groups could be of potential relevance for clinical practice. To be useful, however, this exercise should produce a stable classification, that is, a consistent list of biological groups, independent of the markers studied. So far, that has not been the case (Coop et al. 2009).

## *4.1 Human Population Structure*

A popular approach to the description of the genetic structure of a population exploits an algorithm, STRUCTURE, assigning individual genotypes to an arbitrary number of clusters, *k*. Various *k* values are tested, and their likelihood is eventually estimated. In the first worldwide analysis based on STRUCTURE, Rosenberg et al. (2002) typed 377 STRs in 1056 individuals from 52 populations. Of the six clusters they eventually identified, five corresponded to continents or subcontinents, and the sixth to a genetic isolate in Pakistan, the Kalash. Individuals of the same population tended to fall in the same cluster, or shared similar membership coefficients in two clusters. The authors concluded that self-reported ancestry contains information on DNA diversity, and hence that an objective clustering of genotypes is possible, if large amounts of data are considered.

In fact, clustering is possible, but it is not consistent across studies. In a subsequent paper analyzing a larger assemblage of data, the same authors failed to confirm the Kalash as a separate unit; instead, the native American populations were this time split in two clusters (Rosenberg et al. 2005). The Kalash resurfaced as a distinct group when 15 Indian populations were added to the analysis, leading to the identification of 7 clusters, with most populations of Eurasia now showing multiple memberships. In these studies, all African genotypes formed a single group, a result that may suggest a flaw in the methodology, since there is broadly replicated evidence of high (and sometimes extreme: Schuster et al. 2010) genetic differences between African populations (Hunley et al. 2009). Indeed, when the same dataset was analyzed by a method looking for zones of sharp genetic change or genetic boundaries, Africa appeared subdivided in four groups, and each American population formed an independent group, giving a total of 11 (Barbujani and Belle 2006). In Jakobsson et al's. (2008) study of more than half a million SNPs, STRUCTURE indicated different clusterings if the SNPs were individually analyzed or if they were combined to form haplotypes; in turn, both inferred clusterings were inconsistent with those inferred from CNVs in the same individuals.

In short, no matter whether inferred from old-style protein variation or from recent genomic analyses, the proportion of human genetic variance due to differences between populations is modest. Differences exist and have significant evolutionary implications, but it is an error to consider them typical of populations, and not of individuals, because all populations comprise genetically different individuals. When the number of markers is large, many dissimilarities are detected, and a fraction of these are likely to achieve statistical significance.

However, minor differences in the markers considered, in the sample distribution, or in the method of analysis, lead to different clusterings.

### *4.2 Genomic Consequences of Mismeasures of Man*

A spectacular illustration of what this aspect of human diversity implies comes from a study comparing complete individual genomes. Among the first people whose genome was entirely sequenced are James Watson and Craig Venter, both US geneticists of European ancestry. Their genomes share 1,715,851 SNPs, which is less than each of them has in common with the genome of the Korean scientist Seong-Jin Kim (1,824,482 and 1,736,340, respectively) (Ahn et al. 2009). The fact that a person of Asian ancestry (Kim) is genetically intermediate between two persons of European ancestry (Watson and Venter) does not mean that on average Europeans are genetically closer to random Koreans than to each other, but highlights the limitations of such rough categorizations. Populations are indeed structured in the geographical space, Asians and Europeans generally appear well separated in analyses of population structure, but when it comes to predicting individual DNA features, labels such as “European”, “Asian” and the like are misleading, because the DNAs of members of the same group, Watson and Venter in this case, may be very different. If what matters for future research is whether by racial labeling we can approximate what is in a person’s genome, it is already clear that the answer is no (Xing et al. 2010). As a matter of fact, the only way to know what is in a person’s DNA is to study that person’s DNA. In the past, this task was technically challenging, but now it is both feasible and cheap.

## 5 What’s Wrong with Biological Determinism

In a sense, biological determinism is the consequence of a deep faith in the ability of science to explain everything. Unfortunately, that faith is at present unjustified. To stay within genetics, we understand well how single genes work, and by analyzing DNA we can predict the occurrence of almost all single-gene diseases. However, most diseases depend on the interaction of multiple genes and other factors in the environment. The available models to predict disease onset are rather simple, and become unsuitable when the relevant players in the game (genes, proteins and environmental factors) are more than a handful. That is why we do not have yet any predictive model for the onset of Type 2 diabetes, to which at least 36 genes are known to contribute (Herder and Roden 2011). Greater numbers of genes contribute to causing most cancers, cardiovascular diseases, and neurodegenerative diseases; this also means that the effect of each single gene on the pathological phenotype is smaller, and hence harder to identify (Goldstein 2009). Understanding variation for common traits such as height, weight, or physical performance is clearly more complicated than predicting disease onset (see Weedon et al. 2008 and Goldstein 2009), and an even more complex task is to understand the genetic bases of variation in human cognitive abilities. In a study of gene transcription in the frontal cortex of the brain, more than 1,500 genes have been found to change their level of expression during fetal or infant development (the authors do not give the total number of genes with constant levels of expression) (Colantuoni et al. 2011). This means that, even if what we call intelligence depended only on the genes expressed in the frontal cortex (which is very simplistic), to account for its genetic bases we would have thousands of factors to consider—at present, a totally unmanageable number. Like any other trait, cognitive abilities have a genetic basis, but at present any statement on their inheritance is utterly speculative. Statements on putative genetic causes of cognitive differences between human groups (Herrnstein and Murray 1994) are even less justified.

Scientists have their share of responsibility for the spread of biological determinism. The repeated observation that population affiliation is not a reliable predictor of an individual's specific genotype (Xing et al. 2010), has not led to a deep critical reconsideration of the validity of terms such as "race," "racial differences," and "ethnic background" in medicine. Apparently unaware of 30 years of research in human diversity, Risch et al. (2002) wrote that many genetic studies have come to the identical conclusion that each continent is home to a race, and claimed that they could demonstrate the validity of racial self-categorization "from an objective perspective". In fact, they ended up defending the status of race for Hispanics, a group composed of people of different origins who have two features in common, being immigrants in the US and speaking Spanish, neither of which has any genetic basis. Following Risch et al.'s example, racial categories are routinely employed by US medical doctors, scientists, and in community health. On May 27th, 2013, a PubMed search of scientific literature using the term "human races" returned 141,804 items, and about 1,000 new entries are being added every month.

One reason why US medical doctors hesitate to abandon racial categorizations may be the fact that different diseases have different prevalence in different populations. Actually, much like any other allele, alleles associated with genetic pathologies or predisposition to diseases do vary in frequency. Because these frequencies are also low, these alleles tend to show more restricted geographical distributions, so that many of them can be regarded as population-specific; examples include several hemoglobin variants, the *HEXA* mutation causing Tay-Sachs disease in Ashkenazi Jews, and the Mendelian alleles associated with the so-called Finnish disease complex. However, in all these cases, the pathologic alleles are carried by a small fraction of the chromosomes in the population, typically less than 1.5 %. Defining Ashkenazi Jews as the carriers of the Tay-Sachs disease allele would mean that the 98 % of Ashkenazi Jews who do not carry the *HEXA* mutation should look for a new racial label.

While recognizing that distinguishing groups of humans from each other on genetic grounds is problematic, Harpending (2007) argued that the race concept remains indispensable to understand the causes of human disease. He then proposed to regard as races human groups among which genetic differences exist. Since some degree of genetic differentiation has been found between any two sets of humans compared so far, be they arbitrary, or defined by geographical, cultural or epidemiological criteria, Harpending's definition implies that any human population is a race, which seems to create more problems than it solves. However, above and beyond the semantic problems, insisting on a racial subdivision of humankind seems risky, not only for the reasons explained by Stephen Jay Gould (1981) in *The mismeasure of man*, but also because this leads to poor science.

Ever since the development of a scientific approach to medicine, therapeutic strategies have had the purpose to cure the "average patient". However, much like human races, the average patient is an abstraction disregarding the differences between individuals. On the contrary, real patients have different disease risks and respond differently to pharmaceutical treatment. In a sense, then, the so-called racial medicine is an attempt to come to terms with these differences and somehow take them into account. But it is a scientifically superficial attempt, based on the unjustified assumption that people classified in the same racial category are genetically homogeneous.

Contrary to the claim that racial stereotypes capture some meaningful aspects of biological variation, the available data indicate that to predict whether an individual will have certain health risks or will benefit from pharmaceutical treatment, one must study that individual's genes. Individual drug response varies as a consequence of variation at several genes coding for the enzymes responsible for drug metabolism. In a study of CYP2D6 (Ingelman-Sundberg et al. 2007), the best-known drug-metabolizing enzyme, Chinese and Swedes were shown to differ in their average rates of metabolism, with an excess of slow-metabolizing individuals in the Swedish sample. However, both populations included the whole range of possible phenotypes, from poor to ultra-rapid metabolizers (Johansson et al. 1991; Shimizu et al. 2003); once again, we are observing what Stephen Jay Gould observed in Tiedemann's skulls. Therefore, a racial-medicine approach consisting in looking for a dosage of the drug that will make everybody happy in Sweden or China is a waste of time. What is conceivable and, in the future, hopefully feasible, is to identify the alleles responsible for individual variation, hence giving to each person, no matter whether Chinese or Swedish, the drug dosage that fits the individual therapeutic needs.

## 6 Tentative Conclusions and Future Prospects

Population-genetics theory and empirical data show that genetically differentiated groups tend to evolve when genetic drift affects populations connected by little or no migratory exchanges. In that case, the populations' internal diversity will decrease as alleles are lost by chance and seldom reintroduced by gene flow; because in each population different alleles are lost and different mutations occur, genetic boundaries may arise. Conversely, boundaries are unlikely to develop if the effects of gene flow exceed those of drift, in which case each population will contain variable proportions of alleles coming from elsewhere.

All humans are genetically different, but our species shows lower degrees of inter-population differentiation than all other widespread mammal species (Templeton 1998). Geographical patterns in human genome diversity exist, but each human population harbors a large share of the species' diversity; that diversity is basically continuous in space, rather than interrupted by boundaries. All this probably means that population subdivision was more the exception than the rule in the human past, and that admixture phenomena prevailed on those promoting isolation. The fact that no agreement has ever been found on the number and definition of human races is a consequence of this kind of evolutionary history.

Now that hundreds of whole genome sequences have been studied, there is no reason to suspect that the comparatively weak geographical structure of humans might be an artifact, due to our limited ability to detect the alleles that make us, apparently, so different. If we are to understand our demographic history, a good starting point is thus to ask what combination of evolutionary factors has led to the coexistence in the same populations of a broad spectrum of genetically different individuals. This way, we might be able to reconstruct aspects of our migratory history that still escape us. The fossil record documents an origin of anatomically modern humans in Africa, more than 100,000 years ago; we do not know yet if they expanded through Palestine in a single wave, some 60,000 years ago (Ramachandran et al. 2005; Liu et al. 2006), or if there was an earlier exit through a Southern route, i.e., through the horn of Africa into Southern Asia and Australia (Lahr and Foley 1994). A better understanding of the times and tempos of dispersal from Africa is crucial for testing the hypothesis of a possible (if limited) hybridization between anatomically archaic and anatomically modern humans, recently supported by the publication of a draft sequence of the Neandertal genome (Green et al. 2010). Finally, different hypotheses exist on the details of the peopling of several areas of the world, and by carefully investigating current and past genomic diversity we might be able to reject some of these hypotheses.

It is hard to see how the race concept can still be regarded as a useful tool for addressing these and similar questions. However, race does remain an important component of our social and psychological world. This component affects human interactions and social policies, and will not vanish just because some scientists say it has no objective basis. In a sense, then, races exist, and should be kept into consideration. However, on the basis of what is known, they exist only in the sense that the labels we stick on ourselves and on the others have practical consequences, even if they do not correspond to empirically identifiable biological realities (Glasgow 2009). Should new biological evidence emerge, this conclusion will be reconsidered. However, at present, the burden of the proof is definitely on those supporting the existence of a racial structure in the human species. We should all be aware that the persistence of a racial paradigm in some sectors of research and medical practice guarantees that man will continue to be mismeasured, and that prejudice will keep finding pseudoscientific justifications.

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# Affect Bursts as Evolutionary Precursors of Speech and Music

**Klaus R. Scherer**

**Abstract** Most evolutionary science studies the development of morphological changes between and within species, focusing on the fossil records. The development of behavioural changes receives much less attention, possibly because of the relative lack of historical behavioural records. However, it was the father of evolutionary science himself, Charles Darwin, who started the enquiry into the evolution of behaviour when he published *The expression of the emotion in man and animals* in 1872. This was probably the most important pioneering work in this area, not only for the study of emotional expression, but for theory and research on emotion in general. Indeed, this book has catapulted the subject of emotion into the forefront of academic interest and made it a topic for interdisciplinary investigation in its own right.

## 1 Darwin's Three Principles of Emotional Expression

In this publication, Darwin's fundamental thesis was that the expression of emotion serves an adaptive function. He proposed three principles that underlie the production of emotional expression: (1) the principle of serviceable associated habits, (2) the principle of antithesis, and (3) the principle of actions due to the constitution of the nervous system (Darwin 1872/1998, pp. 28–29). There are a number of possible examples to illustrate these principles. An example of the principle of serviceable habits is the expression of eyebrow raising where, for our ancestors, this habit served the purpose of increasing the field of vision, but for modern man it is used when attempting to remember (as if we "could" see what we were recalling), although the expression itself does not contribute to the

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purpose of recall. A possible example to illustrate the second principle of antithesis is the gesture of shoulder shrugging as an expression of yielding. This appears to have no use and is a passive expression that is the opposite of aggressive expression. Habits such as foot and finger tapping are candidate examples for the final principle, where a build-up in the nervous system causes a discharge of excitement. Vocal expressions and expressions of anger are also examples of the third principle, especially as it is only under extreme conditions that animals tend to vocalize in response to pain and fear.

## 2 Comparison to Gould and Lewontin's Spandrel

Darwin's formulation of these principles is quite reminiscent of Gould and Lewontin's (1979) *spandrel* analogy. The spandrel was originally an architectural term used to describe the curved areas of masonry between supportive arches that were also employed for decorative purposes. Their initial inclusion in the design was solely due to a decision about the shape of the arches rather than an artistic judgement and, as such, their decorative purpose was a by-product of their architectural purpose. Gould and Lewontin's concept of a "biological" spandrel describes a phenotypic characteristic that is a by-product of the evolution of another characteristic rather than a direct product of adaptive selection. This is most obvious in Darwin's third principle, where the expressive and communicative behaviour is the by-product of the "nerve-force" generated by physiological arousal.

In trying to show how his three principles contribute to the development of emotional expression in man and animals, Darwin demonstrates the phylogenetic and ontogenetic continuity of certain types of expressive behaviour, with a particular focus on the facial and postural musculature. For example, in the case of phylogenetic continuity, he argued that the similarities between the "sneer" of a contemptuous human and the raised lips and exposed canine teeth of a snarling dog both communicate a similar state of emotion, and both have adaptive value in the context of social interactions within groups.

In this chapter, I will attempt, in an admittedly speculative fashion, to extend Darwin's approach to emotional expression. I will start with the central function of emotion in preparing appropriate action tendencies in response to relevant events and argue for a central role of a very primitive type of emotional expression—affect bursts—in the parallel evolution of both speech and music. While Darwin focused mainly on the face, I will consider here the important role of the voice, arguing that the phylogenetic continuity of *vocalization* as a channel of emotion expression may provide important information for the emergence of speech and music in the human species. One of the most remarkable similarities between animals and humans is the tendency to produce different kinds of vocalizations under conditions of strong affective arousal, traces of which are even found in human languages in the form of interjections (Scherer 1994), which are discussed further below. This interesting phenomenon did not escape Darwin's attention and he provided some pertinent examples, for example, "…, *under the feeling of contempt or disgust*, *there is a tendency*, *from intelligible causes*, *to blow out of the mouth or nostrils*, *and this produces sounds like pooh or pish*" (Darwin 1872/1998, pp. 92–93).

These interjections take different forms in different languages. Thus, disgust over rotten food is expressed "yuck" in English and as "iii" in German. One reason may be that different types of adaptive disgust reactions and the accompanying sounds have been used: "yuck" as part of spitting out the offensive matter and "iii" as closing the nasal pathways to bad odour. Another reason might be the integration of these primitive affect sounds into different languages and the adaptation to the respective phonetic structure, as suggested by Wundt (1900; see Scherer 1994).

So could this disgust interjection be an example of a behavioural spandrel? Darwin clearly thought that expression followed adaptive actions of the body. For example, in the case of disgust, the avoidance of bad odour or bad taste is a normal kind of instinctive reaction, and the vocalization that follows is a by-product in the sense discussed in other contributions to this volume. However, this by-product takes on a very particular kind of function in the context of social interaction, both within and across species, by informing the observer of the state of the expressor and their respective action or intention to act (Scherer 1992, 1994). Once a behaviour has acquired this communicative functionality, then this function obviously becomes an object of evolutionary selection, as Darwin showed with many examples. This begs the question of whether the yuck expression is a "pure" spandrel since the analogy suggests that the vocalization should serve no functional purpose before it becomes a by-product of the avoidance response. However, the emotional expression may well have served a communicative function before its association with the avoidance function; that is, it was already a product rather than a by-product of evolution, in which case this indicates a co-evolution of two existing functions that become associated in one behavioural and emotional expression. This debate remains difficult to resolve due to the problems in separating the different functions and extracting their paths of evolution.

## 3 Primitive Affect Bursts as Precursors to Speech, Language, and Music

Although the "spandrelness" of emotional expression is difficult to decipher, I do claim that, based on the notion of the selective advantage of communicating emotion through motor expression, primitive affect bursts may be the precursors, not only of emotional expression in humans as we know it today, but also of speech, language, and music. This is still a very controversial topic. At one time the French Academy of Sciences banned the discussion of the origin of language because there was so much debate on the subject and very little to advance the debate, and this is still the case. There are very many different accounts or theories of the origin of language and of the origin of music, and many of the protagonists are not well disposed towards other theories (Ball 2010; Arbib 2013). In the early 90s I suggested that one might reasonably speculate that both proto speech and proto music might have used affect vocalizations as building blocks (Scherer 1991). This hypothesis is not unreasonable considering how humans use affect vocalizations and vocal emblems as a means of communication, for example, when we are unable to produce speech or when we use the same conventionalized affect vocalizations across different languages, such as the wailing patterns in mourning rituals. One of the earliest sources for this idea originates from Herrmann von Helmholtz: "*An endeavour to imitate the involuntary modulations of the voice and make its recitation richer and more expressive*, *may therefore possibly have led our ancestors to the discovery of the first means of musical expression*, *just as the imitation of weeping*, *shouting, or sobbing*, *and other musical delineations may play a part in even cultivated music (as in operas)*" (Helmholtz 1863/1954, pp. 370–371).

Helmholtz is very explicit about the link between affect bursts and music, and Darwin makes heavy use of Helmholtz in his discussion of vocalization (except for the origin of music where Darwin preferred his own theme of sexual attraction; see the chapter by Menninghaus, this volume). Similar ideas have already been implied in the work of Rousseau and Herder, and so this idea is not new and I make no claim of originality. However, the role of affect and emotion in the evolution of speech and language appears to have been forgotten by recent theorists and it urgently needs restating. This is surprising since this notion does not conflict with other potential determinants that have a role in evolution, such as gesture. Indeed, other theories on the origin of language and music are easily combined with the account proposed here, as will be shown below.

## 4 Stages in the Evolution of Emotion

To put this into context, I will provide a rapid overview of the evolution of emotion, as this is strongly linked to the evolution of the expression of emotion.

### *4.1 Decoupling*

The origins of emotion are probably best understood as what was primarily called "instincts". For example, the sight of the red belly of a stickleback immediately "releases" attack behaviour by other sticklebacks, a classic case of a direct stimulus-response mechanism (Tinbergen 1951). Examples of instincts closer to the human experience are our reactions to sweet or bitter taste, where there is usually an immediate tendency to approach the sweet-tasting substance and avoid the bitter-tasting substance, probably generated by matching the bitterness or sweetness to various organized patterns of behaviour in our repertoire. Newborn infants, about 2 or 3 h or maybe days after birth, will respond differentially to sweet and bitter taste (Ventura and Mennella 2011), and so it appears to be an emotional response that does not need learning. The same is true in apes and in mice (Berridge 2003). This is a very classic and well studied principle and provides the basis of Lorenz's proposal of the innate releasing mechanism (Lorenz 1981). These fixed links between certain types of stimuli and certain types of reactions serve the stickleback, mice, and newborn babies well and are all that is required for a variety of basic functions. However, they are not as functional in the modern human world, which is far more complicated than that of the stickleback. I propose that emotions started to evolve when there was a *decoupling* of the first part of the mechanism and the response; that is, rather than the stimulus automatically producing the same response in every case, there is an evaluation of the stimulus before the response rather than an immediate execution of the response (see Scherer 1984, 2001).

## *4.2 Appraisal*

The execution of a response may depend on a number of other factors, such as additional information or the type of situation, and it may be disadvantageous to act upon impulses immediately. People who are very impulsive tend to execute their instinctive responses straightaway and this can have undesirable consequences. By providing an appraisal process, emotions can help us make a better choice of action than the responses that may have been produced by built-in instincts.

The organism has needs and goals and it will evaluate or appraise the nature of a stimulus with respect to those needs and goals. For example, the organism will appraise whether the stimulus is new or familiar and whether it is good or bad. If the stimulus is familiar, then the organism should know how to deal with it and respond appropriately, depending on whether it is good or bad. However, if the stimulus is not familiar, then its response may be primarily governed by whether it appears good or bad for the organism's needs or goals and, if it is bad, it will appraise whether it can deal with it. The organism must also appraise the different response options, such as whether to flee or fight, with the best alternative possibly depending on the situational context.

It is only after these various stages of appraisal that there is a response. This fundamental appraisal mechanism has replaced instincts by decoupling the stimulus-response sequence and replacing it with what we now call emotion. There is much disagreement about the exact definition of emotion, and I argue that it is a state of synchronization of different bodily systems that prepares a number of alternative responses, but that it does not in and of itself decide on the execution of the response. It is my personal view that emotion does not include execution; for example, if you have aggressive behaviour following anger, then that behaviour is a different phenomenon and is not part of the emotion. Anger is the emotion, but the aggressive act is one of several responses and the production of an expression of anger may provide enough warning of the aggressor's potential action to avoid a confrontation so that no actual action is required.

## 4.3 Utilitarian, Social, and Aesthetic Emotions

After the decoupling of stimulus and response, I propose that the second evolutionary stage was the development of what I call *utilitarian* emotions such as anger, fear, joy, disgust, sadness, shame, and guilt. These types of emotions are considered utilitarian, as they facilitate our adaptation to events that have important consequences for our well-being by providing alternative responses to the event.

After utilitarian emotions, I suggest there is a further step in the evolution of emotion, which is the development of social and aesthetic emotions. These are not only influenced by our individual goals, but also by our cultural norms and artistic values. Indeed, social emotions are central to my proposals: after the appraisal process there is a special stimulus evaluation check, which includes checking the compatibility of a behaviour with the social norms or rules of society or with a personal self-image. This check further differentiates the appraisal outcome and extends the range of possible action tendencies. Emotions such as shame and guilt are particularly relevant to the social checking process, as shame involves checks against self-ideals whilst guilt involves checks against social norms. The development of these different checks would be part of the evolutionary sequence, which raises the important issue of the timing of the emergence of this mechanism, which will be discussed in more detail in the next section.

Aesthetic emotions are one evolutionary step further again and are linked to experiencing beauty, such as the emotions we feel when in the presence of a work of art or listening to music or prose. These may have developed when humans "had time on their hands" to produce artistic works and to respond to art, but it remains a matter of debate as to whether aesthetic emotions serve a function. It could be argued that the aesthetic emotional response is similar to the response to a peacock's tail or to the mating rituals performed by birds of paradise in that the reaction to beauty serves the ultimate function of procreation. However, if this is the case, the functionality of aesthetic emotions and their role in evolution is complex to decipher. Is it a couple's admiration of the same piece of art that serves the procreational function, or the attraction to the artist themselves, or does the heightened state of arousal caused by the aesthetic emotion serve procreation?

## 5 Rate of Evolution

The processes discussed above may have developed gradually or there could have been a punctuated equilibrium, where suddenly the instinctive mechanism no longer served its purpose and a new mechanism arrived very rapidly and developed from that point. Evolutionary scientists have fossils to provide data on the development of physical and genetic characteristics but, until the emergence of photography and film, behaviour did not leave traces, which means we have to reconstruct plausible behavioural patterns. However, there is one indicator that suggests the evolutionary development of behaviour was between a sudden change and gradual development. This indicator is the continuing existence of the rudiments of earlier mechanisms that used to govern our behaviour, particularly in the case of impulsive behaviour (e.g., outbursts of rage that defy culturally imposed self-control requirements). As such, the evolution of emotion appears to follow a general mechanism in behaviour where there is not a total replacement but elements of the old mechanism continue to exist while the new mechanism develops.

In fact, this is reflected in the structure of the brain. The limbic system is an early ancestral part of the brain that is largely responsible for emotion. This still exists but has been superimposed by layers of the neocortical structure, which have higher control over the limbic system. As such, one could argue for a compromise between the fundamental idea of a gradual ladder-like evolution towards something higher, and a mechanism that triggers more rapid development under certain types of needs such as changes in the habitat. More extreme triggers for development that have been cited are meteorites and climatic change. In order to cope with these colossal events, we may have required better social cooperation or empathy skills to survive and this would put demands on the development of an emotion system, probably leading to an accelerated development once a new principle has been found.

This is what I propose happened in the case of emotion: when the stimulus-response chain was decoupled and replaced by a flexible system of adaptive reactions to relevant events by appraisal-driven emotion, a number of design features for the emotion mechanism were needed that required rapid evolutionary changes. Table 1 shows examples of the evolutionary pressures that could be expected.

Some of the design features of emotions, such as the rapid detection of relevant events, the preparation of highly synchronized response organization, connected multi-modal signalling, and recursive monitoring of what goes on in your body, require the development of certain structures in order to evolve. Given the current emotion system, especially in many mammalian species, sufficient evolvability must have existed to allow the rapid development of the structural requirements for these design features.

**Table 1** Evolutionary pressures on the development of the emotion mechanism (adapted from Scherer 2013)

| Design features | Necessary evolutionary changes |
|---|---|
| Rapid detection of relevant events and evaluation of expected consequences (often in the absence of sufficient information) | More powerful analysis and evaluation mechanisms (with respect to memory, learning, association, inference, and prediction), particularly the development of more fine-grained appraisal checks (e.g., attribution of causality, compatibility with social norms and values) |
| Preparation of highly synchronized response organization in the service of adaptive action | More flexible motor control systems for exploration and manipulation responses |
| Connected multi-modal signalling of reactions and intentions to the social environment | Complex circuitry for sending and receiving socio-emotional messages, especially a high degree of voluntary control of vocal and facial expression for the purpose of strategic communication |
| Constant recursive monitoring through reappraisal, response adaptation, and emotion regulation | Integrative brain representation of appraisal results and somato-sensory feedback of bodily reactions, accessible as conscious feeling, for regulation purposes. Development of the capacity of categorization and labelling of feelings for social sharing |

## 6 Development of Necessary Brain Structure and Functions

If this is the case, is it possible to draw some hypotheses about the types of changes in brain structure and brain function that would have been necessary to accommodate those features? One of the arguments often raised against these appraisal theories of emotion is that the proposed mechanisms are *too* cognitive for an affective phenomenon such as emotion and require too high a level of thought and reasoning. However, Leventhal and Scherer (1987) demonstrated that appraisals can occur on different levels of cognitive input, such as sensory-motor (relating to both sensory and motor functions), schematic (relating to an organized pattern of thought and behaviour), and conceptual (relating to higher level representations). The sensory motor level requires only a minimal level of information-processing ability and many animals will be able to do this in terms of innate preferences and responses to basic needs, as is the case for primates, many mammals, infants, and newborn infants. The schematic level is also likely to be operative for many animals, whereas humans are probably the only species able to process on the conceptual level, as this requires brain functions such as consciousness and logical erudition.

I propose that the development of emotion in individual development (ontogeny) mirrors that in species development (phylogeny). In fact, Hebb (1949) argued that species that possess more complex capacities for cognition will also have more complex emotions, which is exactly my point. Table 2 shows an attempt to predict when certain emotions should start appearing in the infant. The predicted age of onset in months of certain emotions, as proposed by developmental psychologists, is related to the types of stimulus evaluation checks or appraisal criteria. For displeasure and startle, the onset is extremely early because the equipment for appraisal in terms of novelty and pleasantness already exists within the infant, whereas the development of other emotional expression takes much longer. Thus, the stimulus evaluation check against norms and compatibility with the self-concept probably does not occur earlier than 18 months because there is no self-concept before that age and so emotional expressions requiring this type of check will not be in place.

We have tested some of these predictions in a large-scale study with infants between 5 and 14 months of age (Scherer et al. 2004). In this study, an experimenter talked to a baby and the experimenter's voice was then made very deep by activating an acoustic filter, producing a sudden change in voice quality. The study observed gaze direction and freezing as responses that indicate the appraisal of sudden acoustic change. The results for gaze direction towards the experimenter suggest that there is little response to expectancy violation before the age of 7 months and a massive effect occurs only at 11/12 months, indicating a sudden development of the cognitive capacity to discover the origin of the changing voice. These data support the notion of a critical period between 9 and about 11 months in which there is a complete restructuring of cognition with the emergence of new competencies. One can assume that the same sequence of development can be expected for the phylogenetic case, as in the ontogenetic case illustrated above, that is, animal species that are able to attribute causes to events will have a certain level of cognitive capacity, and thus certain types of emotional reactions, whilst species that cannot assign causality will lack this cognitive and emotional capacity.

**Table 2** Stimulus evaluation prerequisites for the ontogenetic development of emotion (adapted from Scherer 1982)

| | | Stimulus evaluation checks | | | | |
|---|---|---|---|---|---|---|
| Emotional expression | Age of onset (in months) | Novelty | Intrinsic pleasantness | Goal/plan relevance | Coping potential | Norm/self-concept compatibility |
| Startle | 0 | × | | | | |
| Displeasure | 0 | • | × | | | |
| Surprise | 1–3 | • | • | × | | |
| Joy | 3–5 | • | • | × | | |
| Anger | 4–6 | • | • | × | × | |
| Fear | 5–9 | • | • | × | × | |
| Shame/guilt | 12–15 | • | • | • | • | × |
| Contempt | 15–18 | • | • | • | • | × |

Regarding the results of the freezing responses, the study found that infants at 5 and 7 months of age will freeze when the voice suddenly becomes very deep, but it found no evidence of the surprise reaction, that is, raising of eyebrows, as Darwin and Ekman have predicted. I propose that this is because there is no cognitive capacity at this age to deal with such a sudden and unpredictable event. The pattern of reaction changes with age, as the freezing response lessens after 7 months and then increases again later on when more capacities are available and the infant can better understand events. However, at the age of 5 and 7 months the expression is one of stupefaction (see Scherer et al. 2004), where the infant stares dumbly at the cause of the startle but is confused and cannot assign any emotional value such as surprise. In other words, in both ontogeny and phylogeny, the degree of cognitive capacity for appraisal determines the nature of the emotion and of the respective expression produced by an event.

## 7 Expression of Emotion as Part of the Appraisal Process

Figure 1 shows the principles of the emotion architecture put forward in my Component Process Model (CPM) of emotion, which proposes that following an event there is a multi-level appraisal of its implications, followed by the generation of action tendencies based on the appraisal outcome. However, it must be remembered that these are action *tendencies* and that they only produce overt motor expression when combined with physiological response patterns.

Figure 2 shows a more detailed illustration of the sequential cumulative process of appraising an event and the effects it has on the other organismic systems, such

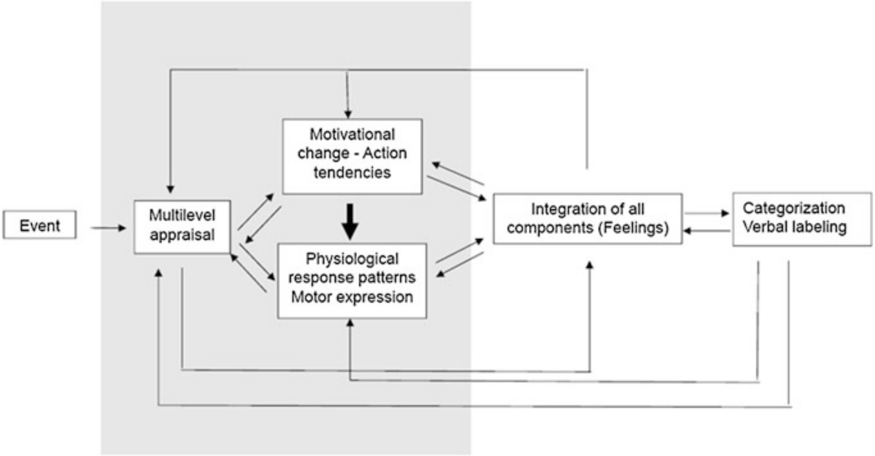

**Fig. 1** Architecture of the component process model of emotion (adapted from Fig. 1 in Scherer 2009)

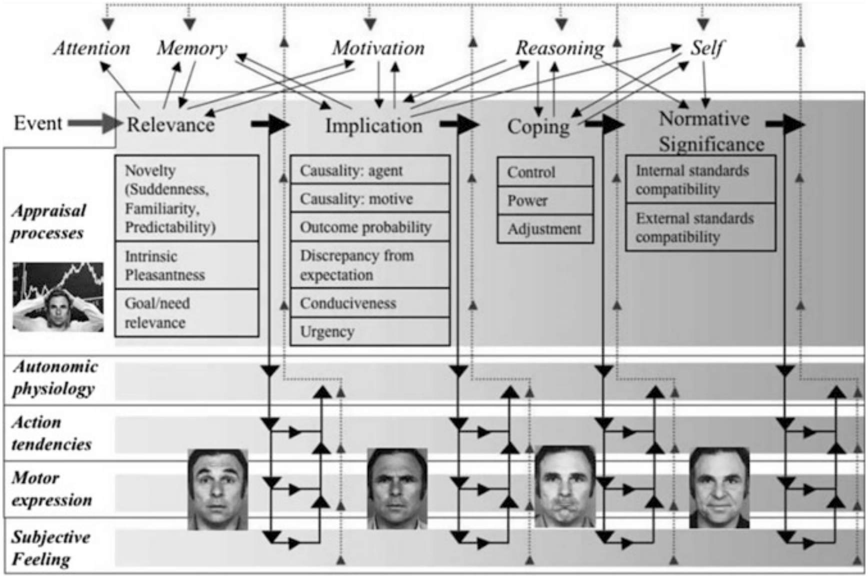

**Fig. 2** The sequential process of appraisal checking and the triggering of efferent responses in different emotion components (component process model; adapted from Fig. 2 in Scherer 2009)

as the autonomic nervous system and the motor system (responsible for expression). It uses the example of a trader discovering a sudden dramatic drop in the stock market. First the trader appraises whether it is relevant and, having decided it is, the trader appraises whether it is novel and important. From this he reasons he may lose a lot of money, and this would obstruct his goals. He then appraises whether he can cope with the stock market drop and, since he has enough money and resources, he decides he can deal with it. Finally, he appraises the event in terms of normative significance and self-concept, for example, whether it would be considered unfair by himself or others.

At each instance of the stockbrocker's appraisal, the process will immediately produce an efferent change, conducting impulses downstream from the central nervous system. As such, there will be an effect on the physiology and on expression but, unlike what Darwin might have thought but never said, that is not the emotion as a whole. Contrary to the assumption of Tomkins (1962) and Ekman (1992), I doubt the existence of innate "neural motor programs" that automatically produce prototypical emotion expressions, and I postulate that the expression is generated "online" and continuously throughout the appraisal process. To complement the facial examples shown in Fig. 2, Table 3 shows some of the predictions of the efferent effects of certain appraisal results on vocal expression.

**Table 3** Predictions of the CPM for the effects of appraisal outcomes on vocal expression (adapted from Scherer 1986)

| Check | Production | Type of voice | Acoustic parameters |
|---|---|---|---|
| Pleasant | Faucal and pharyngeal expansion, relaxation of tract walls, vocal tract shortened due to AU 25 action | “Wide voice” | Increase in low-frequency energy, F1 falling, slightly broader F1 bandwidth, velopharyngeal nasality, resonances raised |
| Unpleasant | Faucal and pharyngeal constriction, tensing of tract walls, vocal tract shortened due to AU 15 action | “Narrow voice” | More high-frequency energy, F1 rising, F2 and F3 falling, narrow F1 bandwidth, laryngopharyngeal nasality, resonances raised |
| Not relevant | No change | - | - |
| Relevant and consistent | Overall relaxation of vocal apparatus | “Relaxed voice” | F0 at lower end of range, low-to-moderate amplitude, balanced resonance with slight decrease in high-frequency energy |
| Relevant and discrepant | Overall tensing of vocal apparatus | “Tense voice” | F0 and amplitude increase, jitter and shimmer, increase in high-frequency energy, narrow F1 bandwidth, pronounced formant frequency differences |
| No control | Hypotonus of vocal apparatus | “Lax voice” | Low F0 and restricted F0 range, low amplitude, weak pulses, very low high-frequency energy, spectral noise, format frequencies tending towards neutral setting, broad F1 bandwidth |
| Control and high power | Chest register phonation | “Full voice” | Low F0, high amplitude, strong energy in entire frequency range |
| Control and low power | Head register phonation | “Thin voice” | Raised F0, widely spaced harmonics with relatively low energy |

## 8 Multifunctionality: Push and Pull Effects

As highlighted by Charles Darwin, the expression of emotion in voice, face, and body is a central feature of emotion, as it has important signalling characteristics. However, we must make a distinction between the primordial evolution of emotion and the more complex tuning of the emotional response by social influences. In emotion expression, this can be called the distinction between *push* and *pull* effects, respectively. Until now, I have focused on the push effects (e.g., the vocal effects in Table 3) which account for the occurrence of spontaneous affect burst as a consequence of certain appraisal results. A nice example is provided by chimpanzee vocalizations in a dominance fight where the vocalization of an animal gives a continuous readout of its emotional reaction. The farther away the subordinate animal flees from the dominant animal, the more forceful and less frequent the vocalization becomes, providing an immediate read-out. In humans this is more complicated because, except for affect bursts like “oh”, we mainly use speech. Since the voice is only active when we speak, the push effects occur when an event changes our speech quality.

Pull effects on expression constitute a fundamentally different mechanism and cause us to produce what society requires of us in terms of conventionalized expression rules in a particular situation, for example, the smiles of politicians during an election campaign. When the need for social control becomes important, we have to use motor control to socially regulate our affect bursts or the push effects. This requires a whole machinery of monitoring, rules, and control structures, in terms of muscle innovation, which requires a more complicated brain organization than required for a simple push architecture. Thus, we need to clearly distinguish between spontaneous and voluntary production, otherwise known as push versus pull, raw versus regulated, or conscious versus unconscious.

The expression of an emotion in the sense of the push represents the authentic state of the expressor, reflecting his/her appraisal of the event that has just happened. However, the expressor could also have fabricated the expression to manipulate the observer or, alternatively, the expressor may have used the expression as a reference or symbol, comparable to the use of emoticons in emails for commentary. An observer can interpret this expression as a direct indicator of a true emotional state but cannot be certain that it is not just a reference to an ideal state or a strategic device as part of impression management.

## 9 Theoretical Underpinning of Multifunctionality

The German psychologist Bühler (1934/1988), in his Organon model of speech, highlighted three different functions of speech: symptom expression, symbolic reference, and appeal to the listener (see Fig. 3).

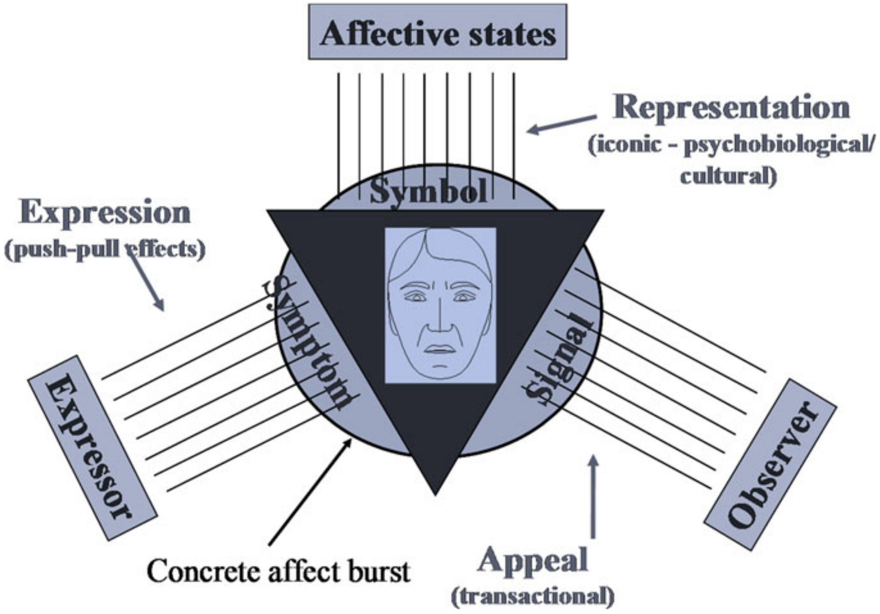

**Fig. 3** Bühler's organon model: the tripartite function of affective expression

The push and pull effects influence the function of expression, whilst the appeal function highlights the fact that expression often affects the observer, changing his or her behaviour. In the case of symbolic representation (due to iconicity, psychobiological associations, or shared cultural rules), the expression becomes a symbol and thus becomes independent of an actual interaction between expressor and observer. The ability to use expressions as symbols allows the emergence of nonverbal communicative systems. This, of course, is an essential precondition to the emergence of language, in that language cannot exist without symbolic reference. Clearly, this function is not limited to language, but also exists for nonverbal expression and, more recently, for emoticons used in emails as symbols of facial expressions of emotions. Despite the rampant neglect of Bühler's tripartite function model in many contemporary discussions about language or nonverbal expression, it is important to highlight the importance of the multifunctionality of expression.

Another important, yet sadly neglected, insight is Brunswik's lens model of expression (Brunswik 1956). Figure 4 shows my attempt at combining Bühler's Organon model with Brunswik's lens model in the form of a new Tripartite Emotion Expression and Perception model (TEEP; Scherer 2011). The emotion of the sender is encoded in distal indicator cues; for example, emotion can be objectively coded in the face by different facial muscle action units and it can be coded in the voice by acoustic parameters. Following the transmission to the observer from the face and voice via light waves and sound waves, respectively,

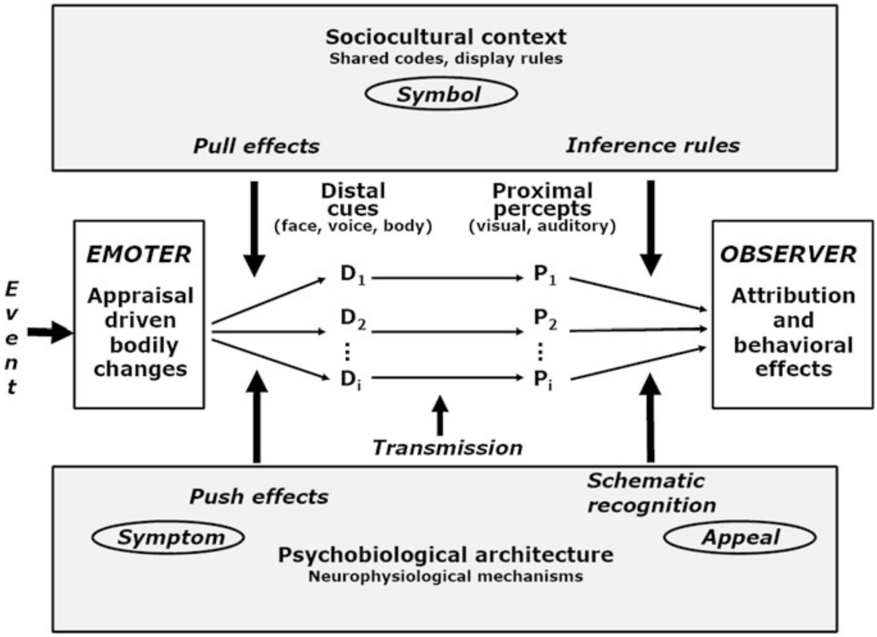

**Fig. 4** Tripartite emotion expression and perception model (TEEP) (adapted from Scherer 2013)

they are registered as proximal cues by the receiver, which serve as the basis for inference or attribution of sender states. The model also shows the determinants of the push effects in terms of neurobiological mechanisms and the determinants of the pull effects, in terms of the encoding and decoding of social rule structures. The ellipses in Fig. 4 illustrate the links between the elements of the process model and the functions proposed by Bühler, that is, symbol, symptom, and appeal.

## 10 Affect Bursts as Precursors of Speech and Music

Above I have outlined my proposals for the architecture of emotion and the multifunctionality of emotional expression, but I still need to explain how this leads to the claim that primitive affect bursts are plausible precursors to speech and music (see also Scherer, 2013). One essential argument is that expression of emotion and impression (or impact) of emotion are very closely linked, as shown in the TEEP model. Leyhausen (1967), a student of Lorenz, showed very early on that expression and impression have interacted strongly during the course of evolution. An impression will lead to conventionalization and ritualization of an expression, which is the source of symbolization described above. Obviously, the process is slow and gradual, but once the basic elements of emotion representation in affect bursts were in place, there could have been a period where the symbolization process developed very rapidly. Expressive signals are shaped by constraints such as transmission characteristics and limitations of sensory organs, distinctiveness, and ease of processing. The operation of pull effects facilitated by social pressure for regulation and the resulting flexibility probably fostered the evolution of abstract symbolic language and music systems, which co-evolved with brain functions and brain complexity.

It is also important to note that an essential aspect of that development is the multi-modality of the expressive signal. Affect bursts are eminently multi-modal, consisting of a synchronized expression in the face, the voice and the body, the arms, and the trunk. In consequence, it is likely that affect bursts are not only the origin of speech and music, but also the origin of dance and other kinds of arts.

## 11 Evidence Supporting Affect Bursts as Precursors

Recent theoretical proposals and empirical evidence have helped establish the plausibility of this claim, in particular, the evolutionary continuity of affect vocalizations, showing that anatomical structures for complex vocalizations existed before the evidence for the presence of representational systems such as language. In what follows, I will give a brief sampling of suggestions in the literature and empirical data that support the claim made in favour of affect bursts as the origin of speech and music.

Brown (2000) suggested a common precursor of music and language, which he called musilanguage, adopting a very similar approach to my earlier suggestion

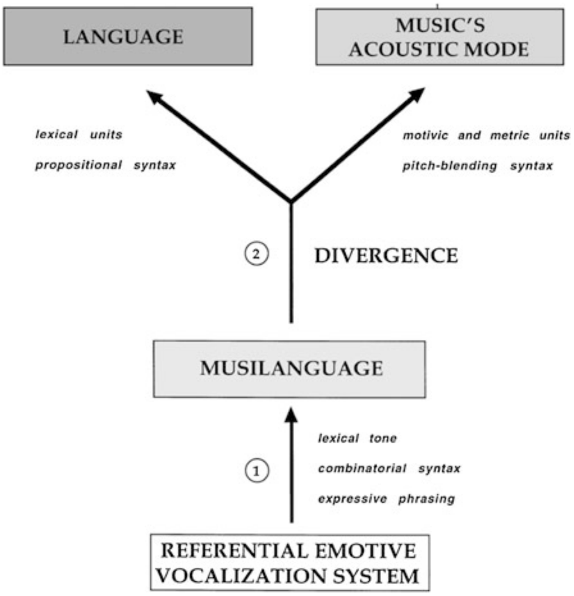

**Fig. 5** "Musilanguage" as a common origin of speech and music (adapted from Fig. 16.5 in Brown 2000)

**Table 4** Vocal affect universals

| Affective-motivational state of sender | Acoustic characteristics of animal vocalizations or human affect bursts |
|---|---|
| Relaxation, contentment, comfort, play | Repeated short sounds with relatively low frequencies |
| Dominance, hostility, agonistic intention | Low-frequency sounds, harshness, falling frequency |
| Defence, fear | Short tone-like calls with rising frequency, high amplitude onset, and broad frequency spectrum |
| Submission, resignation | High-frequency, tone-like sounds with repeated frequency shifts |

(Scherer 1991). Figure 5 demonstrates how a referential emotive vocalization system—corresponding to push effects—produces musilanguage and then diverges into separate strands of language and music that evolve in parallel. Brown also assumes that a simple "acoustic mode" of music which resembles nonverbal vocal affect expression precedes the "vehicle mode" of music, which includes things like musical narration, iconicity, ritual events, and context switching and has presumably been influenced by language structure. Interestingly, there are many traditions of folk song in the world that do not use words and/or contain elements of affect bursts. Similarly, the anthropologist Mithen (2005) in his book *The Singing Neanderthals* has argued that these proto-hominids had a proto-musical language: the "Hmmmm" communication system.

A strong piece of evidence is the clearly documented phylogenetic continuity of affect vocalizations. The ethologist Morton (1977) has identified a set of "motivational structural rules" that he has demonstrated for many mammalian species, showing how changes in pitch contour and vocal energy form continua of increasing aggression and increasing fear or appeasement. Research on the acoustic characteristics of human vocal expression (Scherer 1985, 1986; Goudbeek and Scherer 2010) shows very similar patterns. Table 4 shows an attempt to summarize the effects of affective motivational states of the sender on acoustic phenomena across many different species.

More evidence in support of the claim that affect bursts are the common precursor for the expression of music and speech is provided by the apparent similarity of emotion signatures in both. Thus, Juslin and Laukka (2003) in a meta-analysis of about 200 studies demonstrated the extraordinary number of shared acoustic cues between emotional speech and music (see Table 5).

Another interesting avenue of study is the onset of referentiality in animal vocalizations. One important breakthrough was the work of Seyfarth et al. (1980) on referentiality in alarm calls in vervet monkeys, which shows the acoustic differences between a leopard call, an eagle call, and the snake call. The authors forcefully argued that the call system of primates is not just motivational or emotional, but that it already has a rudimentary referential function.

Another interesting piece of evidence concerns the estimation of the nerve canal size from fossil record, which provides a rough estimate of the increasing size of

**Table 5** Shared acoustic cues between emotional speech and music (Juslin and Laukka 2003)

| Emotion | Acoustic cues (vocal expression/music performance) |
|---|---|
| Anger | Fast speech rate tempo, high voice intensity/sound level, much voice intensity/sound level variability, much high-frequency energy, high F0 pitch level, much F0, pitch variability, rising F0/pitch contour, fast voice onsets/tone attacks, and microstructural irregularity |
| Fear | Fast speech rate tempo, low voice intensity/sound level (except in panic fear), much voice intensity/sound level variability, little high-frequency energy, high F0 pitch level, little F0 pitch variability, rising F0 pitch contour, and a lot of microstructural irregularity |
| Happiness | Fast speech rate tempo, medium–high voice intensity sound level, medium high-frequency energy, high F0 pitch level, much F0/pitch variability, rising F0/pitch contour, fast voice onsets/tone attacks, and very little microstructural regularity |
| Sadness | Slow speech rate/tempo, low voice intensity/sound level, little voice intensity, sound level variability, little high-frequency energy, low F0 pitch level, little F0 pitch variability, falling F0/pitch contour, slow voice onsets/tone attacks, and microstructural irregularity |
| Tenderness | Slow speech rate/tempo, low voice intensity/sound level, little voice intensity/sound level variability, little high-frequency energy, low F0 pitch level, little F0 pitch variability, falling F0 pitch contours, slow voice onsets/tone attacks, and microstructural regularity |

nerves and thus presumably of the development of improved sensitivity and control. While the evidence about the typoglossal canal, leading to the tongue, is contradictory (Kay et al. 1998; DeGusta et al. 1999), the role of the canal for nerves to the thorax, presumably involving breathing control, seems promising. Both modern humans and Neanderthals have wide canals, whereas *Homo ergaster* has narrow canals typical of other apes (MacLarnon and Hewitt 1999). Johansson (2005) argues that our ancestors, not less than 500,000 years ago, already had the anatomical architecture needed to produce the sounds that we can produce today, establishing the existence of a necessary antecedent to the evolution of real language in the sense of a symbolic system.

Further support for the above hypotheses comes from the work on the evolution of the brain. Porges (1997/1999, 2001) argues for the central role of the development of a brain stem regulatory centre, particularly the vagal system, that allows the regulation of emotion and expression of emotion which he believes to be subserving a special “social engagement system”. He argues for the development of a more advanced form of the brainstem regulatory centres that is directly linked to an expanded ability to express emotions. More specifically, he suggests that the somatomotor components of the vagal system contribute to the regulation of behaviours involved in exploration of the social environment (e.g., looking, listening, ingesting) and behaviours involved in acknowledging social contact (e.g., facial and head gestures, vocalizing). This “social engagement system“ would be able to determine the proximity, social contact, and quality of communication, as well as create the ability to regulate emotion in general, which is required for smooth social interaction and collaboration.

## 12 Conclusions

I propose that emotional expressions, in the form of multi-modal affect bursts, are possible precursors to the evolution of speech and music. I believe this suggestion is sufficiently plausible to deserve further attention. I will end with some comments on a Gouldian perspective, relating to spandrels and punctuated equilibria, which raise questions that require continuing research.

Emotional expression through multi-modal affect bursts could have originally been a spandrel of the emotion architecture that served the complex physiological preparation of different adaptive action tendencies and the broadcasting of these through externalization via motor expression mechanisms that are part of the emotion system. However, once the information potential was realized, the communication function becomes an exaptation or co-optation and possibly an object for adaptation and natural selection. Although the evolutionary time course is difficult to predict, it might be possible to find indications of this in fossil and genetic records.

The movement of emotion representation to concept representation in language is most probably a direct consequence of preceding development. Once the principle of representation is acquired, there is likely to be a very rapid extension. This may well be a candidate for punctuated equilibria but also for adaptation, selective advantage, and natural selection of individuals. It is most likely that representation co-evolved with brain development and this may be traceable in the fossil record.

An important question to explore is when, in the course of evolution, music and speech split up and why. This period is also a candidate for punctuated equilibria, an issue that needs to be developed. A particularly important question concerns instrumental music and the invention of musical instruments: when was the first instrument used and when did people first start to make music using methods other than drumming on surfaces?

I conclude with a point about the multi-functionality of speech and music, which is a never-ending debate and brings me to the closing suggestion that many of today’s developments imply that a new point for a punctuated equilibrium may be approaching. The development of musical instruments took a long time, but the inventions of personal electronic musical devices such as the Walkman, iPhones, iPods, and iPads seems to be much faster and this development may well accelerate in the future. Nowadays many people report that they need music in order to work and this could be another function of music, that is, providing an appropriate acoustic environment for different types of activities. If this is the case, then has this function of music been selected or is it a spandrel? These debates will continue and although definitive answers are unlikely, they can provide deeper insight into the evolution of emotional expression, music, and language, possibly allowing us to understand future developments as they happen.

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# Darwin's Theory of Music, Rhetoric and Poetry

**Winfried Menninghaus**

**Abstract** This essay on Darwin's evolutionary theory of human music, rhetoric and poetry will first portray the way Darwin conceives of human music in relation to his animal model of artful singing. Second, it discusses the evolutionary heritage from previously evolved musical capacities Darwin diagnosed in verbal language, more specifically in its artful elaboration in rhetoric and poetry. Darwin's speculations are boiled down to two testable hypotheses: (1) Rhetorically enhanced messages should be aesthetically more appealing, recruit more attention, and result in stronger affective involvement than the same messages deprived of the rhetorical extra-charms. (2) Affective responses to rhetorically enhanced versus rhetorically flat messages should moreover facilitate associations of an at least latent sexual dimension, and/or lead to different responses to sexual primes. In the third section of the present article, empirical studies are partly reported and partly envisaged that have a potential to test these hypotheses. Throughout this essay Darwin's hypotheses are projected onto Stephen Jay Gould's typology of evolutionary processes as well as onto older traditions in rhetoric, poetics, and aesthetics.

## 1 From Sexual Singing to "Mental Reversions to the Emotions of a Long-Past Age": Darwin's Theory of Human Music

Darwin's animal model of the vocal arts (Darwin 1981) stipulates that artful singing and dancing evolved as a feature of sexual courtship that determines sexual choice and in the end reproductive success. Contrary to what is widely understood as Darwin's theory of human music, he has never claimed that this animal model

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applies to *Homo sapiens* without major qualifications. While Darwin's contemporary readers were fully aware of the substantial difference between Darwin's animal model of artful singing and of his take on human music (cf. Stumpf 1885, but also Kivy 1959), more recent evolutionary biologists have routinely oversimplified Darwin's theory of the human arts.

The first such difference amounts to a classical example of what Gould called an "exaptation" (Gould and Vrba 1982; Gould 1991). Darwin expressly relegated the hypothetical applicability of the animal model to what he used to call our "half-human ancestors" or "semi-human progenitors" (Darwin 1981, II 334–337). He suggested that in one of the human lines preceding *Homo sapiens sapiens* the vocal capacities found in gibbons and several other non-human primates may already have been driven to a high degree comparable and even functionally equivalent to sexual bird-song. In recent years, this hypothesis has found increasing support among evolutionary biologists (Richman 1987; Geissmann 2000; Hauser 2000; Fitch 2006). At the same time, with regard to *Homo sapiens sapiens* himself/herself Darwin diagnosed a long-since begun dissociation of artful singing capabilities from their putative evolutionary function of promoting sexual success. Darwin even completely refrained from speculating about new functions this "exapted" trait might have acquired, be it in biological evolution or in cultural history (Darwin 1981, II 333).

Instead, he devoted all his efforts to showing that it actually *is*, or at least might be, an exapted trait the neural and vocal machinery of which survived the loss of its putative evolved function of origin (Darwin 1981, II 330–337). Darwin developed his argument primarily by extrapolating a dimension of emotion expression in sexual singing and by furthermore tracing the enigmatic persistence of this dimension of emotion communication in later cultural music. For Darwin, the sexual courtship scenario of artful singing is associated with sexual desire, competition with rivals, uncertainty, tender devotion, occasionally triumph, and a broad array of other emotions (Darwin 1981, II 335). In the most recent human line, Darwin surmised, this link with a whole range of emotions survived the dissociation of the trait from its presumed originary function for sexual courtship (Darwin 1981, II 335–337).

It is precisely this putative persistence of the affective dimensions originally tied to the older context of sexual singing that, at least in Darwin's view, accounts for much of the strong affective impact music and artful speech can leave behind. Moreover, this decoupling of an old emotional heritage from its hypothetical function of origin makes the respective emotions somewhat enigmatic, difficult to decipher, to label and to explain. This whole line of argument is very similar to how Darwin's book on *The expression of emotions in man and animals* (1872) traces forgotten and barely intelligible origins –that once were adaptations of some directly practical use– for many other features of emotion expression. Accordingly, Darwin actually integrated his take on the musical powers of *Homo sapiens sapiens* into his account of human emotion expression (Darwin 1965, p. 217).

Darwin's hypothesis regarding the human vocal arts strongly bears on a key and much-discussed issue in philosophical aesthetics, namely the question why mere sound patterns can strike us as highly emotionally moving while at the same time it is very difficult for us to determine which intentional emotions exactly we feel in this state of music-elicited emotional agitation. Drawing on Kant's theory of "aesthetic ideas" rich in association yet never fully graspable through conceptual definition (Kant 1987, § 49), on German Romanticist versions of this theory and on Spencer's essay "The Origin and Function of Music" (Spencer 1858) which is strongly informed by this tradition (for a more detailed treatment of how Darwin inscribed himself into these contexts, see Menninghaus 2011, pp. 96–114), Darwin arrived at the following hypothesis as to what exaptation has made of the music-related emotions that in sexual singing contexts once had clear intentional references and a clear function:

> As Herbert Spencer remarks, music arouses dormant sentiments of which we had not conceived the possibility, and do not know the meaning; or, as Richter [i.e. the German poet Jean Paul Friedrich Richter, W.M.] says, tells us of things we have not seen and shall not see."[…] The sensations and ideas thus excited in us by music, or expressed by the cadences of oratory, appear from their vagueness, yet depth, like mental reversions to the emotions and thoughts of a long-past age. (Darwin 1981, II 336)

This theory of music's puzzling effects on our emotions—notably, powerful effects in the absence of the functional stipulations of the animal model—is the centerpiece of Darwin's evolutionary theory of human music. In direct contrast to Spencer who attributed the relative cognitive elusiveness of music-elicited emotions to a utopian orientation towards a yet unavailable refinement of emotional communication, Darwin explained this feature as an evolutionary vestige, as the persistence of a long-since forgotten intentional reference of the respective emotions:

> All these facts with respect to music […] become intelligible to a certain extent, if we may assume that musical tones and rhythm were used by our half-human ancestors, during the season of courtship, when animals of all kinds are excited not only by love, but by the strong passions of jealousy, rivalry, and triumph. From the deeply-laid principle of inherited associations, musical tones in this case would be likely to call up vaguely and indefinitely the strong emotions of a long-past age. (Darwin 1981, II 336–337)

## 2 Rhetoric and Poetry as Transformations of Musical Prosody and Related Affects in Verbal Cognitive Language

Darwin's distance from any simple adaptationist account of the human vocal arts becomes even greater, as he moves on from music to rhetoric and poetry. The topical understanding of this move is yet another instance of a systematic distortion, or simply non-reading, of the pertinent paragraphs of Darwin's book *The descent of man, and selection in relation to sex* (1871). Darwin does by no means suggest that symbolic verbal language is a later offspring of music (cf. Fitch 2006, pp. 470–474, 2010). The reverse is true: Very much in line with Herder's (Herder

1985) and other eighteenth century authors' hypotheses of a twofold origin of language, namely of separate evolutionary roots of language's cognitive and affective dimensions (cf. Menninghaus 2011, p. 117), Darwin made it crystal clear that verbal language entails features of symbolic cognition that require an evolutionary explanation on their own and cannot be conceived of as an offspring of any music of the bird song-type (Darwin 1981, I 54, 57).

The only evolutionary descendance Darwin did stipulate concerns a very specific dimension that he suggested to be partly shared by music and speech: namely, features of phonetic prosody and, more specifically, the grip on our affect system by means of phonetic harmony, cadences and other means of sound patterning (Darwin 1981, II 334–337). Darwin held that artful prosodic emotion expression in music is older than verbal language and that in this regard verbal sound patterning recruits the vocal and neural machinery that first evolved for musical sound patterning (cf. Maess et al. 2001; Koelsch et al. 2002; Patel 2003, 2008). Darwin wrote:

> The impassioned orator, bard, or musician when with his varied tones and cadences he excites the strongest emotions in his hearers, little suspects that he uses the same means by which, at an extremely remote period, his half-human ancestors aroused each other's ardent passions. (Darwin 1981, II 337)

Fully conforming both with ancient rhetoric and with Romanticist notions of poetry, Darwin identified the artful elaboration of the musical dimensions of language—its "varied tones and cadences"—as the proper domain of rhetorical theory and poetics. Accordingly, it is not language altogether, but exclusively its artful elaboration which he aligned with the hypothetical proto-music that may have preceded language.[1]

From a Stephen Jay Gouldian perspective on more holistic "architectures" and "*Baupläne*" that shape evolutionary trajectories (Gould and Lewontin 1979), Darwin's theory of the arts of rhetoric and poetry takes the exaptation of vocal music to a second degree. Human music, according to Darwin, has retained barely understood emotional traces of the long-since obsolete sexual courtship contexts that hypothetically shaped techniques of elaborating musical meter, harmony and melody in many species. Human language retains traces of these traces even in the completely different and evolutionarily novel domain of symbolic cognition. Seen in this light, Darwin's hypothesis regarding a musical heritage of language may well be read as suggesting that a random constraint on verbal language—namely, preexisting patterns of musical sound structuring, or, put in a more general fashion, of the vocal and neural architecture of human emotion expression—may play an important role in explaining not why verbal language altogether evolved, but why verbal language entails musical dimensions and why the emotional powers of musical sound patterning may have carried over to linguistic sound patterning.

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[1] Therefore, the criticism voiced, for instance, by Stephen Mithen that Darwin's theory of language cannot be correct because it cannot explain the cognitive and symbolic features of human verbal language as a "derivative of music" (Mithen 2007, p. 26) is completely missing the mark.

Just like in the case of music, Darwin left undiscussed the question which evolutionary or other functions, if any, rhetoric and poetry might serve. This abstinence from suggesting any adaptive story is all the more remarkable, since traditional rhetoric readily provides a functional hypothesis—one, moreover, that Darwin clearly was aware of. Standard rhetorical theory stipulates that rhetorical elaboration of the linguistic signal provides functional benefits for winning over and persuading other individuals or entire groups. From this perspective, it would have been very easy to jump to the conclusion that emotion regulation by means of rhetorical prosody is a sound adaptive successor to persuasion by sexual singing. However, for the time being, it is far from clear whether the persuasive function of rhetoric can, in fact, be understood by recourse to the action of natural selection for enhanced communicative skills.

In any event, the arts of rhetoric are widely understood as techniques of message enhancement that yield a stronger grip on our attentional systems, support a stronger emotional involvement as well as inherent processing pleasure, and, in the end, strengthen the power of persuasion. Ever since Gorgias (Gorgias 1972) and Plato (1925, p. 261a), these psychagogic powers of rhetoric and poetry have been compared to mood-altering and attitude-changing drugs. Notably, erotic seduction by rhetorical means is among the oldest paradigms highlighting the usefulness of elaborating the linguistic signal rhetorically (Gorgias 1972). To promote the sender's interest is in the end the goal of all rhetorical expenditure, whether in the courtroom, public debates or other communicative contexts. Following Darwin's speculations, an evolutionary theory of rhetorical skills is called for that is not coextensive with a theory of language altogether.

Regardless of how useful rhetorical message enhancement may be, Darwin's tracing of its potential evolutionary descendance can well be read as suggesting that it might not have evolved as an adaptive trait directly responding to functional demands, but as a by-product first of the exaptational dissociation between musical practices and sexual choice and second as a coincidental spreading of musical prosody—or of parts of the general architecture of temporal vocal sound patterning—into cognitive language. Again, Darwin completely refrained from offering a story of natural selection for adaptive value, even though the functional benefit of rhetoric appears fairly obvious. Rather, he devoted much care and a very complex line of argument to retracing a story of exaptation and constraints of the architecture and of the emotional underpinnings of preverbal human prosody on verbal language.

## 3 Empirical Evidence

Darwin's model of the musical, primarily prosodic heritage of rhetoric and poetry and of the affective underpinning of this heritage is not only a highly intriguing and interesting contribution to the theory of rhetoric and poetry. It is also perfectly testable. It entails two predictions:

(1) Rhetorically elaborate messages should be aesthetically more appealing, recruit more attention, and result in stronger affective involvement than the same messages deprived of the rhetorical extra-charms. (They should, for these very reasons, also have a better access to memory.)
(2) Affective responses to rhetorically enhanced versus rhetorically flat messages should moreover facilitate associations of an at least latent sexual dimension, and/or lead to different responses to sexual primes.

Obviously, the second aspect is the more critical and distinctive one. Unfortunately, our (yet unfinished) empirical studies on effects of rhetorical patterning have not yet reached the point where I can present data on this second aspect. The first aspect, however, is also far from being trivial, since to date there is very little empirical research on the processing of rhetorical patterning and poetic language (Hoffstaedter 1987; Hanauer 1998; McGlone and Tofighbakhsh (1999, 2000); Van Peer 2002; Hakemulder 2004; Zyngier et al. 2007; Lea et al. 2008). For instance, McGlone and Tofighbakhsh (1999, 2000). Findings from our own research thus far lend support to Darwin's hypotheses. In the remainder of this essay I report in a summarizing fashion experimental research designed to measure the aesthetic and emotional effects of the poetic elaboration of ordinary language (cf. Jakobson 1960, on the "poetic function" of language). The critical features manipulated for this purpose were rhyme and meter, and hence two eminent features of musical prosody in Darwin's sense.

Today, very few people are actually used to reading poetry. Nevertheless, our rating studies revealed that experts and non-experts are similarly sensitive even to minute changes of the original lines. The fully poetical versions were indeed attributed significantly higher degrees of *aesthetic liking* and *felt intensity* of processing (Obermeier et al. 2012). Moreover, a yet unfinished fMRI study using the same set of systematically modified strophes selected from German poetry of the 19th and 20th century showed higher activation in the meter and rhyme conditions—compared to the depoeticized versions—for a sustained attention network, for brain areas involved in emotion processing and for structures that have also been shown to be involved in processing musical rhythm (Kotz et al., in preparation). In summary, in line with the first prediction derived from Darwin's hypothesis, we found significant meter and rhyme effects in terms of aesthetic liking, intensity of affective involvement, and affinities of processing between music and poetic language. Notably, these effects appear to be pure effects of verbal art, since they are found in a whole variety of different linguistic contexts, including desemanticized strophes.

As to the second prediction stipulated above, we are still in the process of designing several other experiments aimed at manipulating a whole variety of rhetorical and poetical features in different stimulus sets and measuring the concomitant effects. Besides pursuing other hypotheses, we will use all these stimulus sets in order to test whether the presence or absence of features of rhetoricity, or poeticity, actually also primes or facilitates associations related to the affect spectrum of sexual courtship and choice. If this turns out to be the case—even in texts that are content-wise unrelated to sexual courtship—, this would constitute an empirical piece of evidence in support of Darwin's highly inventive hypothesis and of Gould's emphasis on evolutionary trajectories far more diverse and complex than stories of direct selection for adaptive function.

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# Part IV
# Stephen J. Gould and Human Sciences

# Beyond (and Without) the Invisible Hand. Conceptual Shifts Between Economics and the Theory of Evolution

## Andrea Cavazzini

**Abstract** Conceptual shifts and transfers between evolution theory and political economy are the basis of the dominant economic theory i.e., General Equilibrium Theory. Since Adam Smith, classical political economy assumes that equilibrium is the normal and spontaneous result of economical evolution; orthodox neo-Darwinisme assume that equilibrium and harmony are the normal results of biological evolution. A better understanding of economical and biological phenomena may come from "heterodox" theories, such as marxian et keynesian ones, viewing crisis and non-equilibrium as the normal condition of social reality. A confrontation is proposed between these socio-economical theories and theories of life phenomena developed by recent philosophical and scientific research.

The analogical transfers of concepts between the life sciences and the social sciences are not recent phenomena. A particular case of these shifts and intersections between fields of knowledge is the one concerning the relationships between the Darwinian theory of evolution and the classical political economics. In these two areas, the construction of objects and their respective issues was often conducted through reciprocal contaminations in particular as regards the problem of dynamics, i.e., the forms and laws that govern the movements of, respectively, life and socio-economic phenomena. The work of Stephen Jay Gould is particularly important in view of these issues. In the first place because, as a historian of science, Gould often insisted on the importance of analogies and metaphors, and of verbal and figural images, in the construction of concepts: one can safely claim that Gould was a great theorist of what Gilles Châtelet termed 'allusive stratagems', which constitute a part of that 'halo' of imprecision, approximation and

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non-rigorousness whose pre-formal fertility plays a key role in the formation of concepts (Châtelet 2010). Furthermore, Gould's contribution to the theory of evolution can be seen in the light of possible similarities with some recent developments in the economic theory, certainly motivated primarily by the explosion of the economic crisis and the helplessness demonstrated by the dominant economic science in front of it. In fact, the theory through which Gould transformed the framework of the theory of evolution is the theory of Punctuated Equilibria, and the mainstream economic theory that inspired and still inspires the economic policies is the General Equilibrium Theory. It may be only a case of a verbal suggestion based on a mere terminological misunderstanding. But it may be useful and interesting, on the other hand, to try to understand whether the conceptual changes that seem to imply a problematization of the concept of equilibrium, though occurring in different branches of knowledge, may somehow clarify each other and help to formulate general problems concerning the dynamics of biological and socio-economic phenomena.

We can begin to discuss these issues starting from one of Gould's many contributions to the history of science, dedicated to the relations between Darwin and Adam Smith. More precisely, to the conceptual shift through which Darwin allegedly used Smith's 'invisible hand' idea to build his own concept of evolution (Gould 2002). In one of the opening chapters of his last, great book, *The structure of evolutionary theory*, Gould argues that Darwin resorted to Smith's concept of a collective welfare, which would generate spontaneously out of a non-regulated interaction process between economic actors, each of them pursuing one's own egoistic interests. Collective benefits and their maximization would arise from a selfish economic behaviour, without the need of external regulations, according to a dynamics that goes from bottom up to produce order—that is, broadly speaking, equilibrium—from a purely chaotic interaction. According to Gould, Darwin tried to find out in these ideas of Smith's—which were known to him by their endemic presence in the cultural context where he had been educated, rather than because of a direct study—a way to reverse the natural theology of William Paley, the philosopher, moralist and churchman who had been a pillar of British thought in the first half of the nineteenth century and whom the young Darwin admired and respected. In his *Natural Theology* (1802), Paley had founded his vision of the divine harmony that governs every natural reality on the famous 'watchmaker analogy': if the harmony and the convergence of a clock's elements towards a unique goal demonstrate the intervention of a regulatory intelligence, then the harmony and the convergence towards a consistent functioning of all beings in nature testify to the operation of a divine intelligence that would 'rule' the universe. According to Paley, God intervened directly to design and build the world order, its consistency and the harmonious cooperation of all of its parts. Darwin, according to Gould's reconstruction, tried to prove instead that the phenomena of 'order' and 'harmony' visible in the natural world are only side and surface effects, temporary 'areas' of order and stability, produced as 'drifts,' or 'fringes' of a process without purpose or consistency, from which an order arises only as a contingent effect of a huge production of disorders, 'errors,' deformities and destructions. What seemed to Paley to match the design of a creator, to Darwin is just a by-product of a fortuitous dynamics. What for Paley is a proportioned and consistent *world-machine*, for Darwin is only an 'area' temporarily ordered that stands on an enormous blind process.

Gould is undoubtedly right in thus characterizing Darwinian evolution. But perhaps he exaggerates in attributing the same position to Adam Smith. For the Scottish economist, in fact, the process governed by the 'invisible hand' is far from being blind and contingent. The relationship between Smith and Darwin—or rather, between the classical economics derived from Smith and the evolutionary currents related to Darwin—had already been investigated by John Maynard Keynes in his essay, *The End of Laissez-faire* (Keynes 1926). Keynes intended to criticize the view—typical in the British culture—of a harmony that arises spontaneously from the interaction of individual actions, a view shared by the classical political economics, the philosophy of Locke and Hume, the Darwinists, Bentham and…Paley. Keynes insists that Smith's 'invisible hand' is *not* an operational concept proper to economic analysis, but a theological postulate that Smith used to support a 'natural' and spontaneous coincidence between individuals and communities, between the competitive egoism and the general progress. In this sense, Smith fully shares Paley's theology and metaphysics. If Keynes is right, Gould was not sufficiently true to his sensitivity to metaphorical strategies: an 'invisible hand' is still…a *hand*, that is, a regulatory presence introducing at the beginning of the process the conditions of order production which the process itself will be responsible for returning at the end. But in fact, the dynamic process will never produce a result different from what the 'hand'—the manifest and glorious one of Paley's watchmaker or the discrete and hidden one of Smith—had already introduced at the beginning. The production of order in Smith is actually a process of order revelation which is already given since the beginning: the order of a human nature whose manifestation is produced by the 'invisible hand.' In these circumstances, we cannot say that Darwin drew on the social dynamics theorized by Smith to build his concept of contingent evolution, where order and equilibrium are only a temporary stabilization of a contingent process. This is certainly the Darwinian concept—at least in the most fruitful interpretation of it, which Gould decisively contributed to establish—but it opposes *both* Paley's watchmaker *and* Smith's invisible hand (as well as an understanding of the evolution that was common to Spencer, the Social Darwinist ideology and, occasionally, Darwin himself).

What is this opposition about? As we have seen, the 'invisible hand' of Smith and the universal harmony of Paley have one thing in common: the initial data and conditions of the process are considered as complete, definitive and unambiguous, so that the process itself cannot give anything other than what is already contained in the original data. There is no uncertainty, or unpredictability, or contingency, since there is no possible introduction of decisive novelties but only the deployment of what is contained in the initial 'project' (no matter if this project is the work of a visible or 'invisible' author). To find at the end the order given at the beginning, nothing should disturb the course of the process, that is, the initial order must exhaust in itself all possible trajectories of the objects involved (living beings or economic actors). The space of possibilities should be saturated and totalized by the initial data so as to guarantee the uniqueness of the process results. This assumption is expressed by the General Equilibrium Theory in a way that is most clear (and naive, given that, contrary to Smith, his supporters think they can take as a scientific postulate what for the Scottish philosopher was still a theological *petitio principii*): "The hegemonic economic theory depicts the economic system as one in which the *homo oeconomicus* takes his decisions about the future in a position of unlimited certainty and knowledge" (Lunghini 2012, p. 29, transl.). This initial assumption is ultimately a transfer to the economic processes of the universal determinism hypothesized by Laplace: the exhaustion of the possible paths of any object, of which the Laplacian Intelligence is allegedly capable once known their original data and equations of movement, is regarded as accessible in principle to the 'omniscient' economic actors (and in any case to the theory investigating into the achievement of the economic equilibrium). The equilibrium, that the General Theory considers as the result of free interactions between omniscient and utterly rational actors, is indeed given at the beginning and coherently contained in the initial conditions defined by the theory: "The neoclassical theory describes a world in which the *homo oeconomicus* benefits from perfect rationality and unlimited knowledge and where there are neither crises nor distributive conflicts. The market will take care of all this: markets—if allowed to work freely—would be so efficient as to set in motion such movements of prices as to ensure the equilibrium in all markets and in the economic system as a whole. The system would settle in a full equilibrium and, if external shocks move it from there, to that full equilibrium it will revert automatically. The neoclassical world is a homeostatic world, a world able to self-regulate: therefore, a world in which the government agenda in the economic field is empty. Any state intervention would be useless or harmful, and the best economic policy is the *laissez-faire*" (Lunghini 2012, pp. 29–30, transl.). But precisely for this self-regulating process to be possible, a finite and predetermined initial complex of immutable conditions must be assumed: unlimited knowledge and perfect rationality ensure that between knowledge and decision, between decision and action, between action and outcome, there will not be uncertainty areas where discontinuities, innovations, contingency may creep in. The final equilibrium is always the result of the assumption that all possible trajectories are exhaustively predeterminable through an appropriate demarcation of the initial conditions: then we are still in the conceptual universe of Smith. The neo-classical economic theory is based on the assumption that an equilibrium given at the beginning—the perfect rationality and omniscience that place the different actors in a position symmetrical to each other—is reproduced at the end of a self-regulating process as economic equilibrium and maximization of utility.

In contrast, the Darwinian process of evolution—as Gould perfectly understood—is defined exactly by the impossibility of determining in advance the trajectories that the objects can follow. The initial data are not given at all, and that is why the results of evolution are unpredictable. According to Francis Bailly and

Giuseppe Longo, who refer explicitly to Gould, the specificity of biological processes—both at the organism and the macro-evolution levels—consists precisely in the impossibility to define in advance, in the very act of building the object-of-knowledge, what in physics is called *phase space*, which indeed defines the trajectories proper to the system examined (Bailly and Longo 2006). Physical theories—including the quantum theory, where the processes are indeterministic, and the chaos theories, where the processes are deterministic but unpredictable—define the behaviour of the trajectories in a given phase space. On the contrary, in the processes studied by the life sciences—and whatever the level each time considered as appropriate—the phase space is modified in the course of the 'trajectory' of living things. Bailly and Longo speak of a set of different phase spaces that would define the potentials of individual organisms, species, populations, ecosystems, etc. Moreover, these different spaces are modified by the development of the process: the biological 'trajectory'—ontogenetic or phylogenetic—changes the possible initial data that define the trajectories. The appearance of new organs or new species redefine a posteriori and in a circular way the 'field' of possibilities given to living things: "In biology, the theoretical and conceptual difficulty lies mainly in the impossibility of providing an upstream formal global determination and a phase space which could frame the phenomena long enough in time; that is, to describe a global mathematical determination (a set of equations) in a space of phases, i.e., of possible evolutions, given once and for all, or quite". (Bailly and Longo 2006, p. 244, transl.).

If this is the structure of biological processes, and if this structure is radically different from that postulated by the classic 'invisible hand' and the neo-classical self-regulating market, it is perhaps possible to find similarities between this idea of biological evolution and the non-Smithean visions of economic dynamics. The impossibility to define a priori the space of possibilities in the economic processes was theorized by Keynes through a reference to the uncertainty of the action. Since real economic actors are neither omniscient nor perfectly rational, they determine their actions according to (a) their accumulated experience (always provisional and changeable); and (b) the imitation of the behaviour of others—not their actual behaviour, but the one which is supposed to be adopted by the majority of the actors (Keynes 1936). In both cases, the 'field' of possibilities defining future actions may be subject to radical changes under internal and external contingencies. Above all, it can be changed retroactively by the ongoing process: the actions actually undertaken modify the wealth of past experiences accumulated and, consequently, transform what each one can assume as the more plausible behaviour of the majority of the actors. Since there is no continuity between initial data and subsequent actions, the process is not homeostatic. Rather than confirming the invariance of an order through changes that end up self-cancelling out, it passes continuously through massive *transitions* that modify its overall structure. In other words, it is constantly far from equilibrium: trajectories do not simply express the totality of objects and parameters initially given but keep changing them all the time, so that the possible differences continue to arise in the course of evolution.

The levels of organization change, so the situations are never perfectly symmetrical and the constraints imposed on the process can never be predetermined.

We can find a scheme not unlike this in the other great anti-neoclassical, that is, Marx. In the Marxian model of capitalist dynamics—and not of 'economy' in general—the crisis is the normal and permanent status of the process. This is due to the fact that the structure that governs the evolution of the system is not a situation of equilibrium, which would ensure the homogeneity of the process and thus the final production of another equilibrium via self-regulation. What props up the process of capitalist development is the permanently asymmetrical situation called 'class struggle': for the process to be triggered, it is necessary that an initial break in symmetry occurs, consisting in the appropriation by the capital of the conditions of production. At each moment in the process of this appropriation, which is in effect an expropriation, a separation more or less violent of the producers from the conditions of production, must be reproduced (Marx 1867). This 'underground' conflict supports the device—apparently circular and autopoietic—of the valorization of capital, which seems to depend on self-regulation. In fact, the 'virtuous' results of the capitalist dynamics depend upon the aleatory progress of an incessant conflict where no equilibrium is preserved: on the contrary, the Homeostasis of the system, its ability to retain its structure by neutralizing the crises, is in any time and any case a surface effect of a permanently critical situation.

To conclude, we can say that the analogies between economics and life sciences suggest a critique of the assumptions on order and equilibrium in the theoretical construction of dynamic models. In the living world as well as in the historical-social one, relevant processes are not restricted to a mere confirmation of an invariant structure of a complex of possibilities given once and for all: on the contrary, they constantly produce new, unpredictable structures. Going perhaps beyond the technical use of physical–mathematical terminology, we can consider these processes as 'far from equilibrium,' or more directly as 'critical' in this precise sense, that they continuously pass through transitions in which the structures and levels of organization that decide the possible trajectories are constantly changed. These transitions do not preserve the original order along the process, and thus break the assumption—shared by Smith and the General Equilibrium Theory—of a reflection of the initial order in the final optimization. From an epistemological perspective, this view of life and historical processes can be seen as an extrapolation of the theory of extended criticality proposed in Bailly and Longo (2006) and later developed in the works of Giuseppe Longo and his collaborators. From a more general point of view, which is perhaps of some interest for the current affairs, we can affirm that the crisis is the permanent status of phenomena in life and human actions. It is therefore worth trying to think about the implications of it using the adequate cognitive tools, which however—if what we saw in the cases of Keynes and Marx is true—cannot replace or exhaust the meaning and the need for action in a structurally uncertain and conflicting reality.

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# Stephen J. Gould, Between Humanism and Anti-humanism. Neoteny, Exaptation and Human Sciences

**Alberto Gualandi**

**Abstract** The aim of this chapter is to analyze the "effects", more or less expected, that the neotenic conception of human nature, proposed by Gould in *Ontogeny and Phylogeny*, produced and may still have on the human sciences. Showing that man is a primate characterized by a developmental Heterochrony—a primate who "was born a year too early" and that "overexposes" his plastic and premature brain to a social and natural environment for a very long period of development—Gould has opened the way for all a series of cognitive and neurobiological consequences, psychological and linguistic, anthropological and philosophical of which we have not yet taken full measure. As it has been done on the basis of Gould's theories by many scientists, the human brain—because of its high neotenic plasticity—can be considered as an extremely powerful device for the refunctionalization (exaptation) of preexisting biological structures, for purposes other than those selected by evolution. However, it is also possible to show that humans can compensate for the disadvantages caused by this neotenic condition only by establishing a communicative relationship with himself and with the world. Through this communicative relationship, the eye and the hand, ear and voice come to entertain synesthetic intersensory relations, unavailable to any other animal, which the unusual structure of metaphorical human experience and the propositional structure of the human *logos* are based on. It follows a conception of human experience that transcends the traditional distinctions between *Naturwissenschaften* and *Kulturwissenschaften*, and that sheds new light on the condition of man in our times.

In one of his most significant works, David Bohm—the great quantum physicist—observed that the biology and psychology in the second half of the twentieth century were still tied to epistemological mechanistic and deterministic models, completely overcome by the physics of the twentieth century. Although sciences of life and mind are fields of study in which the active and creative character of the

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instances which animate the "undivided wholeness of nature" become more apparent, biologists and psychologists insist on reducing the emerging and hierarchically ordered structures of living nature to molecules, genes, neurons or other supposed elementary particles. The virtualities, potentials and physical gradients that express themselves temporally and spatially, interacting with a living body that is part of this totality, are so reduced to hypothetical ""basic building blocks" out of which everything is made" (Bohm 1980, pp. 19–20). These ideal and mechanical atoms are not actually more, according to Bohm, than imaginary projections, ontological hypostasis of our language and patterns of action of our body. In other words, they are anthropomorphic metaphors.

Although this view is shared in different ways by many scholars educated by the great revolutions in physics of the twentieth century (Penrose 1989; Stapp 2007), we believe that this view does not apply to Stephen J. Gould's biological reflection. Other contributors in this volume committed to showing the novelty of Gould's idea of life, in the light of concepts of virtuality, potentiality, hierarchies of causal levels and networks of nonlinear spatiotemporal relations that closely resemble Bohm's concepts. Rather than examine these issues in order to revise that judgment, however, we would like to focus on a seemingly marginal aspect of the scientific and philosophical production of Gould: his conception of man. This view seems innovative because of two facts. First, it provides us with an image that overcomes not only the determinism still prevailing in life and mind sciences, but also its dialectical antithesis: the idea that the main property of human nature is that of not having one, the idea of a "non-nature" of man. Secondly, this conception of man seems innovative to us because of the "effects"—in part unexpected by Gould himself—that it has produced in a series of border researches, which have made two simple and effective ideas—the concepts of exaptation and neoteny—the cornerstones of a new anthropo-biological model.

Let us briefly consider the first point. The question of human nature is a real front line for contemporary thought, the theoretical front of a war of which Gould, more than any other contemporary author, has highlighted the ideological and political stakes. The fact that this battle is overloaded with ideological and political values does not mean that this issue is hopelessly flawed, or that dealing explicitly with this issue necessarily means, as some assert, to commit the sin of anthropocentrism. Giving this a "positive" response, as Gould has attempted in the last chapter of *The Mismeasure of Man*, means showing that on the one hand if "we are inextricably part of nature", on the other "human uniqueness" cannot be "negated thereby". ""Nothing but" an animal—Gould argued—is as fallacious a statement as "created in God's own image"" (Gould 1981, p. 354). Since, however, Gould's warning was not enough to curb the wrong statements, we must then wonder which instances have come to occupy the two opposite extremes of God and animal in the current scientific-philosophical debate. And why does man feel the compulsive need to identify with what is not, with the *other* of himself, either God or the other animal?

Since Gould directed his criticism against the pseudo-scientific program that is called sociobiology or evolutionary psychology—which claims to bring human attitudes, behaviour and feelings to cognitive and behavioral modules, selected from the species during the evolution and stored in the human genome in the form of discrete packets of information and rules required for the functioning of these robots pre-programmed by nature that are nothing but human beings, as well as every other living thing—the ongoing conflict on the issue of human has further widened, at least as far as philosophy is concerned. Split down between the two opposing sides of the "analytical" and "continental", philosophy is divided into two factions: on the one hand, those who, motivated by a need for modeling cybernetic or formal logic, reduce the problem of human nature to the identification of a "super-mental program", functionalist or connectionist, implementable "at will" in the brain or in the circuits of a powerful computer; and on the other hand, those who, aware of the risks of any formalization, strongly argue that the peculiarity of "human nature, is to have not one", because the human being is the being who builds up his own nature in the course of history, through society, language and culture.

Although it appears to be unitary, this Continental position conceals significant differences, ranging from those who believe that any attempt to raise the problem of human nature in terms of "a what", implies an inevitable "ontological degradation" of "the Who" of the one who interrogates, to those who believe that man is only a " texture effect", or "sign" bound to vanish like a face drawn in wave-eroded sand. This continental position, however, proves to be fragile, especially with regard to current challenges. Habermas's case is exemplary in this regard. In an attempt to argue against "liberal eugenics", the last great heir of the Frankfurt School has been accused by his detractors of making use of a metaphysical concept of human nature that he had dismissed as ideological since the mid-50s, in his critical engagement with the only philosophical movement that had set the question of man on the double track of natural sciences and philosophy: German philosophical anthropology. In short, he couldn't get rid of the problem of human nature, despite the legitimate suspicion and caution of *Critical Theory*.

The case of the great Richard Lewontin shows that even the most sagacious science isn't free from such an impasse. After observing that every theory and practice of political power requires, more or less explicitly, a doctrine of human nature, and after denouncing the ideological use that liberal and individualistic contemporary society makes of biology, and in particular of the reductionist program of sociobiology, Lewontin (in one of his finest works, *Biology as Ideology*) concludes by quoting Simone de Beauvoir: "a human being is "*l'être dont l'être est de n'être pas*" (Lewontin 1990, p. 49). According to Lewontin, only the consciousness of this fundamental fact can return to the human species the consciousness of its responsibilities for action—responsibilities which, for better or for worse, are not given to any other animal, because no other species is given the opportunity to decide its own extinction. What moral should we draw from this paradox after which current biology converges on the same "meta-theoretical negative" positions of continental philosophy?

First of all, it shows us that not even the healthy use—implemented by Lewontin, and, recently, many other authors—of developmental biology, critique of genetic reductionism, and the return to a constructivist and dialectical conception of the relationship between external and internal instances, between genes and environment, against any theory (Darwinian or Monodian), of their rigid opposition, is enough to magically produce a *positive* image of human nature. From a more creative and contingent nature, endowed with temporality and "history" already at the level of the embryonic development of a drosophila or a bee, it does not pass to the question of man in a gradual manner, but only with a metatheoretical jump thanks to which the human nature comes to be thought out properly only by negation: *neither creature of God, nor monkey with a highly gifted brain, nor computational robot*. But how do we respond *positively* to our compulsive need for *identification*?

Let us start from a paradox. Commenting on King and Wilson's pioneering results (King and Wilson 1975), on the minimum difference that separates the human from the chimpanzee genome, in *Ontogeny and Phylogeny* and *Ever since Darwin* (Gould 1977a, p. 405, 1997b, p. 45), Gould noted that the close genetic and evolutionary proximity risks leading to paradoxical difficulty. How can we explain that a small genetic difference, of 1, 4 per cent, may result in a behavioral difference, significant enough to ensure that no monkey will ever write the *Iliad* or the Beethoven's *Fifth Symphony*? On the basis of a hypothesis advanced by King and Wilson, the only solution to this paradox may lie, according to Gould, in genes of special type—variously known as "key genes", "master", "architect"—responsible for a number of cascade effects (anatomical, cognitive and behavioral), distinctive features of the "anthropological difference" between humans and chimpanzees. What are they and where are these genes located? At present, Gould replied, unfortunately we do not know, but we know the way they act by regulating the timing of activation of other protein-coding genes. We also know that, in humans, their effects were described, in the second half of the '20s, by Bolk and de Beer (Bolk 1926; de Beer 1933), in terms of a general slowing of development that allows the human race to preserve even in adulthood twenty-five morphological and behavioral neotenic traits—"nudity", orthognathism, advanced *foramen magnum*, hallux non-rotatable, persistent cranial sutures, shape of the pelvic bones in women, small teeth, prolonged childhood, etc.—typical of the juvenile, fetal and infant stages of the chimpanzee. But there's more. As shown by Adolf Portmann (Portmann 1956), such ontogenetic development is in fact characterized by a *dual heterochrony* in which the *slowed* development phase is preceded by an *accelerated* one, intrauterine and postnatal, that determines, at first, an increase in the rate of development of the brain, and a necessary anticipation (of almost 1 year) of the birth's moment and, afterwards, the slowed and prolonged overexposure of a "premature" and "almost fetal" brain to the human and natural stimuli of the environment. But—we must now pose a question—what evidence has contemporary biology given in support of this hypothesis that Gould proposed in the mid-70s? And also, what kind of philosophical consequences does this heterochronical development, this accelerated/decelerated process of individuation of the human body and brain, produce?

It is known that, in the mid-90s, Gould himself in his last colossal work (Gould 2002, p. 1322), hailed the harvest of results produced in two decades by the newborn

Evo-devo biology, as an experimental genetic confirmation of his earlier heterochronical theories of development and evolution, once forced to return to unidentified regulatory genes. Assumed at first—at the macro-descriptive level—by pioneers such as de Beer, Goldschmidt and Gould himself, these genes were indeed located for a few decades in these Hox genes, and other developmental regulatory genes, which determine, on the one hand, the *Bauplan* of the body of an individual belonging to a given species and, secondly, the timing of activation of other structural genes. Also Bolk, de Beer, Portmann, Gould's hypothesis, that the human being is nothing more than a primate with an accelerated/decelerated development now enjoys a certain credit even among Evo-devo biologists away from Gould's "saltationist heresy" (Gilbert 2003, p. 361; Carroll 2005, p. 107). It is, moreover, shared by contemporary neurobiologists, such as Alain Prochiantz, Steven Rose and Gary Marcus, who offer us precious arguments in support of the philosophical argument (almost Hegelian) that we would like to enunciate here: *the advantage offered by nature to a primate that was born a year too early—which enters the world with an only 23-percent-developed brain, and overexposes its plastic and premature brain to a social and natural environment for a very long period of development—is to consolidate intra-specific and social relations that inscribe in the brain matter the symbolic, language and institutional structures accumulated by species* (in the course of a rapid process of cultural Lamarckian evolution).

Before arguing the "tightness" of this neurobiological argument, we will attempt to briefly clarify its most general psychological and anthropological implications. Using the concepts of the phenomenological psychiatrist Erwin Straus, one could argue that, during the delayed human development, interpersonal relationship with the Other (*heteros*), *precedes* the relationship with the otherness of the world (*allon*) (Straus 1958, p. 68). Consequently, the relationship with the world is dialectically mediated, metaphorized, compensated by the communicative relationship with the *other*. Using the concepts of psychoanalysis, one could argue that the communicative, emotional and nutritional relationship with the other inscribes its structures in the neurobiology of the brain through the mediation—to use the term coined by the U.S. psychoanalyst Donald Meltzer—of the "sensory-motor montages" of the body (Meltzer 1975). In turn, psychoanalytic concepts find a new legitimacy and a new foundation in this anthropo-biological context: the Oedipus complex may also be read as a kind of mythical transposition of the original trauma of premature separation from the womb (Mahler 1968; Melandri 1968; Mahler et al. 1975; Tustin 1972, 1990), and paternal super-ego can be interpreted as the result of a process of "internal socialization", of "communication with oneself", which inscribes its effects in "the inside layers from which the drives echo" (Gehlen 1940, p. 304), in the unconscious itself.

At this precise point, in our opinion, a second argument intervenes, which is vital to understand the "human": the thesis of the neotenic heterochronie requires the theory of the communicative structure of human experience as a necessary complement. In part, this theory is present in the writings by Gould, who supported it by adducing the data provided by Montagu and developmental psychologists such as Passingham, but it can be better clarified by bringing together the analysis provided in the mid-twentieth century by one of the leaders of philosophical anthropology: Arnold Gehlen. According to Gehlen, the human being can indeed compensate for the disadvantages caused by this condition of prematurity and overexposure only by establishing a communicative relationship with itself and with the world. Through this communicative relationship, the eye and the hand, ear and voice establish intersensory and synesthetic relations (Mazzeo 2005), unavailable to any other animal, and to those—as pointed out by the above-mentioned psychoanalysts—in whom such communicative relation fail to be established: people suffering from autism. This communicative relationship triggers off a number of processes of exoneration and refunctionalization of anatomical, neurobiological, and cognitive structures that are the basis, on the one hand, of the unusual metaphorical structure, which Gould as well as cognitive linguists like George Lakoff and Mark Johnson (Lakoff and Johnson 1999; Lakoff and Núñez 2000), attribute to human experience and, on the other hand, of the propositional structure underpinning the deliberative logos of the "rational animal". The human being does not achieve this result because predestined by God or by evolution, but because it can exploit, in the process of cultural "homination", the creative trick that, as shown by Gould, Vrba, and Jacob (Jacob 1977; Gould and Vrba 1982), nature uses everywhere: the exapting *bricolage*, or the exemption of a structure from old tasks and functions, and its reutilization for new ones. Relieved of walking, the hand is, for example, reused for communication purposes, which in turn are taken on by sign and gestural painting, and finally by the voice. In conclusion, the "voice of conscience" is not just a metaphor for deliberative thought that emerges with the rational animal, but the most archaeological trace of a process of biological and cultural evolution, which leads to a stable and effective result only when the phono-auditory apparatus, exempted from phonatory action itself, assumes the role of model and guide of the entire sensory and motor system. Therefore, the consciousness of one's possibility of and responsibility for action, which Lewontin attributed to the human species through a sort of leap into the void, can perhaps be established more gradually.

To justify this collection of theses from the neurobiological point of view, we must go back schematically through three stages I have developed in detail elsewhere (Gualandi 2009).

(a) On the basis of the analysis of contemporary neurobiologists such as Alain Prochiantz and Gary Marcus, we must first highlight the crucial role that development genes play in the processes of differentiation, construction and evolution of the brain, since "the basic model of the brain"—with partitions in hindbrain, midbrain and forebrain, and between right and left brain—is the same in all vertebrates because of regulatory genes (those that produce proteins that regulate the activation or deactivation of other genes) such as *Otx* and *Emx* (Marcus 2004, p. 141). Unlike the *Hox genes*, *Otx* and *Emx* do not follow, however, the rule of colinearity, that is, the topological arrangement of these genes on chromosomes does not correspond to the topological structure of the different sensory and motor areas of the brain. Therefore the sensorimotor

*Homunculus* of Penfield and Rasmussen cannot arise directly from them, but along a track mediated from *Hox* genes which govern the construction of the body. This must be remembered to understand the follow-up.

(b) In the second place, starting from the Steven Rose's analysis (Rose 2005, p. 134), we have to demonstrate that genes such as *FOXP2*, responsible—according to some—for only human cognitive processes such as the propositional language, are not genes that determine the possession of a greater number of syntactic mechanisms and cognitive modules, deputed to specific functions, as evolutionary psychology would like to teach on the basis of the "model of the Swiss boxcutter" or of the "chimpanzees' highly gifted brains". How could that happen—suggests Sean B. Carroll—if in humans, compared to chimpanzees, there are only two different amino acids out of a total of 716 that make up the protein encoded by the gene *FOXP2* (Carroll 2005, p. 264)? They are instead regulatory genes that, acting on the timing of activation of other genes, allow greater brain plasticity and a consequent exaptation of perceptual and cognitive structures already existing in other primates. As Gehlen and Plessner, the leaders of twentieth-century philosophical anthropology, had already guessed, the main feature of the neotenic human brain lies in that widespread "hyperconnectivity" which—according to Vilayanur Ramachandran (Ramachandran 2003)—allows the different sensory modalities to associate themselves through processes of exoneration and exaptation, which create intersensory patterns, synaesthetic and metaphorical relations, unavailable to other animals. These relations are the basis of the symbolic perception and the vocal and graphic language, as well as of the function of feedback/feedforward (Edelman 1989; Churchland 1995; Changeux 2002) that our "quiet conscience" has exapted from that sensory modality that connects us with the *Other* since the earliest days of life: our hearing. With the help of the analysis already proposed by Gehlen by the middle of last century, we can try to provide the first reconstruction, strictly materialist, of the genesis of that phono-auditory structure, which neurobiologists called "superior-" or "secondary-consciousness" and philosophers "self-consciousness". This theory was otherwise confirmed by Straus's phenomenological aesthesiology and Jaynes's Psychiatry (Straus 1958; Jaynes 1976), the audio-phonology and the theories of lateralization advanced by Annett and Crow (Tomatis 1963; Annett 1985; Lieberman 1991; Crow 2004), the study of paleoanthropology made by Tattersall and Corballis (Corballis 1991, 2002; Tattersall 1998, 2002; Mithen 2005).

(c) Going back to the developmental genes and Alain Prochiantz analysis, we could finally show that the sensorimotor montages and intersensory patterns, which allowed humans to speak and think in a particular way, are made possible by the fact that the developmental *Hox genes* affect the brain—leading to the sensory and motor homunculus of Penfield and Rasmussen—only through the mediation of the body, or through the feedback of the peripheral (sensory and motor) system on the central nervous system during the long process of individuation. Contrary to what cognitive psychology claims, we could show that "it is not the brain that thinks, but the body"

> (Prochiantz 1997, p. 157) or, in other words, the brain only acts as a transducer of signals or sensitive interface to the dialectical relationship that the body engages with the world (Lewontin 1991, p. 45). In conclusion, the sensory-motor montages that the human body develops in its historical and cultural relationship with the external environment are placed in the plastic and premature neotenic brain, forming a sort of "outside inside" or "inner world outside" (Gehlen 1940, pp. 231, 298), or—to quote the words of the philosopher of cybernetics Andy Clark—an "objectified prosthesis" or an "external scaffolding" of the human mind (Clarck 1997, pp. 167, 191). Lewontin's conception of a dialectical and interactive relationship, between the internal organism and the external environment, becomes now slightly more precise in the case of man.

But let us pose this question once again: why does the postmodern man feel the need to identify with a cerebral highly gifted monkey, with a computational machine or with an ontological nothing? This paradox can be explained primarily from a fact we already know. According to Prochiantz, the human being lives in the paradox of being "highly individuated" and being at the same time, a "very social individual", an "extreme individual" that, as such, can be constituted in the course of a greatly delayed process of individuation (Pochiantz 1989, p. 78). Because the human brain is born a year too early, lacking those extra-specific coordinations that allow other animals to adapt "instinctively"—through a kind of "genetic memory of the species" (Prochiantz 1997, p. 148)—to species-specific pre-determined environments, the human being can indeed compensate for his "ultra-neotenic" condition of prematurity and overexposure (Mazzeo 2002), only by means of a sort of exaptation or primary cognitive *metapherein*. It can compensate for this condition only by transferring on the external environment the intra-specific coordinations, and the mediated structures of "sense"—intersensory and cognitive, affective and symbolic—linking it, from early childhood, to its peers. We must now notice that this communicative *transfert* has two primary consequences. If, on the one hand, it allows a great adaptive advantage, since it provides the human species with an openness to the world, namely flexibility and plasticity, that no other species knows, and that allowed it to populate the entire globe, keeping its (nomadic) "center" within itself, in its clan, language and culture, on the other hand, it gives rise to a withdrawal into the self and into their "intra-specific coordinations", which is the basis of all anthropocentrism and anthropomorphism, ethnocentrism and cognitive, linguistic, cultural, political transcendentalism. Instead of demonizing it, anthropocentrism can be finally explained as the means by which man compromises with the *Open*. As recently observed by some researchers (De Carolis 2008), if the phase of withdrawal completely prevails over the one of opening, or vice versa, or if there is a clear dissociation of one phase from the other, there will be the rise of those individual and social pathologies that mark our times. Modern's man need for identification of modern man with the machine, with nothingness or the animal provides an example of this phenomenon: partial communicative transfer, or division and rigid expulsion of the opposite pole. The famous case of the autistic child Joey—who identified his organs and his body with a patchwork of machines, created by him, to stay alive and protect himself from the open—is paradigmatic in this sense.

However there is another fact that must be considered to account for this paradoxical need. The intra-specific hereditary coordinations that have enabled the human species to breed a neotenic offspring are not in themselves sufficient to assign a familial or social group's identity to individuals. To know who they are and how they must act collectively, in the course of their history, human groups have needed to identify themselves with symbolic and cultural institutions that have taken each time the aspect of the great wild animal to be hunted, the totemic animal, the god-kings of ancient Egypt, the word of the God of monotheism, the cyber-golem, using a socio-historical logic—an exapting, exonering and communicative logic—similar to the one described above, in order to solve more and more complex needs.

Now, when the last great institutions of the past are wavering, including that institution on which all modern institutions should be based—the meta-institution of language—the human species seems to be faced with the choice of either imploding in its own neotenic nature, by assigning the prehuman semblance of a society of consumerist, couch potato bonobos to the human "fluid mass", or alienating itself completely in its machinic prostheses, enslaving itself to a technoscientific scaffold, completely independent of human rationality. In other words, Nietzsche's prophecy of a humanity divided into a caste of masters and servants—unformed and malleable mass of people enslaved by the media to the technocratic elite that holds the world's destiny in its hands—seems to become an inexorable fate for the postmodern era. The only difference is that the elites in power seem to have now lost that freedom and creativity that Nietzsche still ascribed to them, as they obey a rational-technical language, now completely autonomous, that imposes its own anonymous and impersonal logic on those who are subjected to it, but also on those who use it.

Although rushed, the juxtaposition of the anthropo-biological logic of language with the logic of money can help to better understand what we mean. Just as language allows the body to be exempt from a set of direct experiences of the world by bearing the perceptual contents of the other senses, money allows the farmer not to worry about tomorrow's or next year's hunger, transforming, as Marx showed, some chosen goods into a symbolic universal medium of exchange. It is through this means that the farmer will not have to exchange his wheat crop as soon as he has finished his supply of wood or wine. In modern times, money thus sets itself up in an abstract system of equivalences in which the whole structure of relations that organize business is symbolically transposed: the hardships of work and the cares of need, the use-value of a product and its exchange-value, profit and wages etc. In other words, money, like language, is a technical means, selected by the species to release the body from the needs of the moment, and then exapted to produce more money and, abstractly, accumulate time. Contrary to what Weber claimed, the capitalist society is thus not the result of a religious ethic, historically determined, but, as Marx showed, the effect of a refunctionalization of an interhuman form of mediation that ended up destroying and absorbing any other cultural and political institution. Becoming capital, money has in fact turned into an anonymous subject, into an "emerging social structure"—Gould would say—that pursues its goals in a totally autonomous way. And its being well adapted to the technological society depends on the fact that money itself has acquired the form of a symbolic-numerical mega-machine that, increasingly abstract and self-referential, now thinks for itself, rather than through man's brain.

Something similar can be said also of language. Relieving the body of the direct experimentation of the world—and, in particular, exapting the identifying structure of the haptic sense by means of the name, and the characterising action of the eye by means of the predicate (Tugendhat 1976; Tomasello 2008)—the propositional language becomes the primary means by which the human being, from the great monotheistic religions up to the modern age, experience himself and the outside world. Invented, according to Michael Corballis 50,000 years ago for fun or by accident (Corballis 2002, p. 198), and selected due to its ability to consolidate the inter-specific relationships within the group, the phono-auditory language has a great advantage: it can be refined and tested in early childhood without appealing to any reality other than that of the sound produced by its voice and found to comply with the outcome anticipated in the imagination by its own hearing. But if, on the one hand, this advantage allows man to experience reality on the basis of expectations that he produces autonomously thanks to language, on the other hand, language is likely to lock up the human species in a world of increasingly abstract signs and metaphors separating consciousness from the body, man from man, the human species from nature and from the world. Empowered by writing and infinitely enhanced by digital technologies, the meta-institution of language seems to shatter into a variety of "niches" or "spheres" of meaning (Gould 2001, p. 108), in which every social group and each expert, whether scholar, philosopher or scientist, is imprisoned as a result of a sort of sensorimotor *loop* produced by the ability that the phono-auditory apparatus has to be self-sufficient. In conclusion, what awaits the postmodern man in the new millennium is a kind of collective autism where everyone protects himself in some way against *the open*: that is, against the undivided and becoming Totality that we evoked through Bohm at the beginning of this essay, and that, using Gould's words, we might call, more simply, Nature. Does this therefore mean that a different relationship with Nature, understood as the open or as the "undivided and becoming Wholeness", is more desirable and possible for the postmodern man? Or does it mean that despite our arguments, despite the efforts made by Gould and his followers to positive define what man is, the human enigma is still far from being solved?

It is now obvious to all of you that the gloomy and pessimistic picture that I have just outlined contrasts deeply with the personal and philosophical beliefs that accompanied Gould throughout his human, intellectual and scientific adventure. It contrasts with that belief or conviction that some commentators have rightly defined his Humanism: the idea that the human being realizes itself freely in history, the idea that history holds a meaning that transcends nature, which, as Darwin taught us, in itself makes no sense; the idea that the human being has individual and collective responsibility to plan a better future in history for itself and its fellows (York and Clark 2011, pp. 91, 165, 183; Allmon 2009, pp. 27, 39). As we have tried to show, the image of history and the future that unfolds in the postmodern horizon, however, does not seem to confirm the unlimited creative and self-constitutive potential that Gould attributed to man because of his neotenic nature. Did one who throughout his life struggled more than any other against the closures in the specialized language of science, who more than anyone else tried to offer us a pluralistic and open image of nature, overestimate the man's potential? Or didn't he grasp the intrinsic limitations due to the fact that, in the human being, all freedom is a freedom obtained from nature through nature? That is, obtained by means of a trick that nature itself has taken many times during its course: exaptation? Or didn't he take sufficient account of the fact that denying a sense to nature, in the name of a materialist, contingentist and anti-anthropomorphic conception of nature, makes it extremely difficult to attribute any sense to man? In other words, we must ask, is it really possible to propose—as Gould claimed or attempted—a philosophy of nature which is totally de-anthropomorphized and anti-humanistic, and at the same time appeal to a humanistic image of man as regards the conception that we have of ourselves, of our liberty and our social and historical possibilities? All these questions should be carefully considered, not only by those who are philosophically interested in Gould, but also by those who care about the fate of post-modern man. For the time being, a simple and provisional answer would probably be enough. Neotenic heterochronie and neurobiological and cognitive exaptation are not only conditions of possibility of the human, but also of what has always been present in history and nowadays clearly reveals itself: the inhuman.

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