

Jerry Fodor and Massimo Piattelli-Palmarini**“What Darwin Got Wrong”**

(Draft, not to be quoted or rediffused)

Chapter 3**The return of the laws of form**

In the previous chapter we saw why gradualist adaptationism is marginalized or inapplicable in much of contemporary biology. The discovery of several key factors (from pleiotropy to gene regulatory networks, from internal constraints on adaptation to the evolution of whole ontogenies, from discontinuous switches of polarity in the expression of master genes to genetic epistasis and epigenetics, just to name a few) makes the picture of evolution remarkably complex. These are constraints “from below”, from molecular interactions all the way up to phenotypes. What we are going to see now is an entire spectrum of other factors that have played a major role in evolution and that are alien to adaptation and natural selection. For historical reasons, and for want of a better term, we will call these “the laws of form”. These are constraints “from above”¹, because the mathematical and physico-chemical laws that explain optimal solutions exceed the boundaries of biology and are abstract.

When very similar specific morphologies (Fibonacci series and Fibonacci spirals²) are observed in spiral nebulae, in the geometrical arrangement of magnetically charged

¹ ‘From above’ doesn’t, of course, mean ‘from God’; it implies multi-molecular and multi-cellular factors and abstract formal principles. Nothing else.

² Technical note: In the Fibonacci series each term is equal to the sum of the two preceding ones (1, 1, 2, 3, 5, 8, 13, 21 and so on). Connecting the outer vertices of an ordered pattern of juxtaposed squares that have areas given by the Fibonacci series with a continuous curve, we obtain the Fibonacci spiral. The ratio between two successive terms of the Fibonacci series tends, to the golden mean as a limit, (approximately 1.61803399). Fibonacci spirals are usually formed when the elements of a pattern optimize their disposition with respect to two opposing forces. The presence of Fibonacci patterns is ubiquitous in plants (phyllotaxis) (Maynard Smith, Burian et al. 1985) and two French statistical physicists, Stéphane Douady and Yves Couder, have shown how these arise in nature, in a laboratory experiment (with magnetically charged droplets) and in mathematical simulations, from self-organization in an iterative process. These patterns, realizing optimal packaging solutions, depend only on initial conditions and one parameter which determines the successive appearance of new elements, The ordering is explained by the system’s tendency to avoid rational (periodic) organization, thus leading to a convergence towards an angle dictated by the golden mean. For beautiful figures and a formal treatment, see (Douady and Couder 1992). For a movie clip showing the droplets formation in real time, see <http://maven.smith.edu/~phyllo/Assets/Movies/DouadyCouderExp5.9MB.mov>

droplets in a liquid surface, in seashells ³, in the alternation of leaves on the stalks of plants stems and in the disposition of seeds in a sunflower, it can hardly be that natural selection is responsible ⁴. As we are going to see in some paradigmatic instances, the relevant search space would be so huge that the hypothesis of such solutions having been found by blind trial and error followed by natural selection becomes exceedingly improbable. It is even hard to suppose that some genetic machinery is specifically (one has to insist on this: *specifically*) responsible for coding these forms *as such*. It's vastly more plausible to suppose that the causes of these forms are to be found in the elaborate self-organizing interactions between several components that are, indeed, coded for by genes (protein complexes, morphogenetic gradients, cell-cell interactions and so on) and chemical and physical forces. The latter are vastly more ubiquitous and vastly less modular than biological processes. They transcend the biological subdivisions into species, genera, families, orders, classes and phyla. The vagaries of genetic and developmental factors operating over hundreds of millions of years, together with various *internal and external* levels of selection, must have been exploring the narrow channels allowed by maximization principles that are applicable to biology, but exceed its boundaries.

In the apt words of mathematician Peter Timothy Saunders, someone who has been criticizing standard neo-Darwinism for many years and has insisted on the importance of the laws of form (Saunders 1980), biologists have to delimit the realm of

³ Logarithmic spirals are commonly observed in mollusks, brachiopods and some foraminifera, as remarked already by D'Arcy Thompson and later analyzed mathematically and empirically by David M. Raup, Steven Jay Gould and A. Michelson (for an analysis and a rich bibliography, see the already cited review by Maynard Smith, Brandon et al. 1985; see also (Raup 1966, 1967))

⁴ Zexian Cao and colleagues at the Chinese Academy of Sciences recently used stress engineering to create differently-shaped microstructures just 12µm across with a silver core and a SiO₂ shell. They discovered that if the shells were encouraged into spherical shapes during cooling, "golden" triangular stress patterns formed on the shells. On the other hand, if they were encouraged into conical shapes, spiral stress patterns were formed. These spiral patterns were Fibonacci spirals. Their comment is that biologists have long suspected that the branching of trees and other occurrences of the Fibonacci sequence in nature are simply a reaction to minimize stress, they say that their experiment: "*using pure inorganic materials may provide proof to this principle.*" Cao et al. in *Physics Web* 2007. (Li, Ji and Cao 2007)

possible creatures first, and only then ask about natural selection: “*The primary task of the biologist is to discover the set of forms that are likely to appear... [for] only then is it worth asking which of them will be selected.*”⁵

Another main advocate of the importance of the laws of form in biology, Stuart Kauffman, rightly (and somewhat sadly), says, in the preface to his important book: “*No body of thought incorporates self-organization into the weave of evolutionary theory*”⁶

As we are going to see, there are good reasons for this divorce, though a recent and still somewhat *sporadic* return of the laws of form into biology may be conducive to some integration in the years to come.

A little bit of history⁷

The monumental pioneering work of D’Arcy Wentworth Thompson launched the very expression ‘laws of form’ in 1917 (reprinted and edited by Tyler Bonner in 1992) (Thompson and Bonner 1917/1992). He made the prescient suggestion that biologists had overemphasized the role of evolution, and underemphasized the roles of physical and mathematical laws in shaping the form and structure of living organisms. In many ways his vast and ambitious work was premature, because the discovery of the biochemical and genetic bases of growth and form were still in the future, and because the mathematics mobilized to explain the phenomena was inadequate.

A few years later, in 1924, the Italian mathematician Vito Volterra (later summarized in a monograph in French (Volterra 1931) and the American mathematician Alfred J. Lotka (Lotka 1956/1924)) independently and convergently discovered the

⁵ (P. T. Saunders, (ed.). (1992). In his preface to *Collected Works of A. M. Turing: Morphogenesis*. London: North Holland: p. xii).

⁶ Stuart A. Kauffman, (1993). *The Origins of Order: Self-Organization and Selection in Evolution*, Oxford University Press.

⁷ It’s of some historical interest that the great German poet and naturalist Johann Wolfgang von Goethe, inspired by Plato’s theory of eternal and changeless forms, and by Spinoza’s doctrine of an infinite combination of “modes”, had the idea of *Urpflanze*, the archetypal forms after which all other plants are patterned. However, the modern scene actually starts with D’Arcy Thompson.

differential equations regulating the oscillatory equilibria of predators and preys in ecosystems, and applicable also to sustainable rates of growth, birth and mortality rates, biochemical cycles and rates of energy transformations, and even the evolution of human means of transportation and fluctuations in financial markets. These equations soon became staple food for mathematical ecologists and theoretical chemists the world over, and still are. Only very recently some timid links with genetic networks have been tried out (REFERENCE).

The importation of the laws of form into biology proper had to wait several decades. In 1952, Alan Turing tried to explain biological patterns on the sole bases of canonical equations of chemical diffusion (Turing 1952 reprinted 1992)⁸. This long-forgotten paper had, in hindsight, major flaws⁹ and the development of molecular genetics ever since the late Fifties paid no attention to it (with the exception of the British geneticist and embryologist Conrad Hal Waddington, cited by Turing in his paper, to whose work we will return shortly).

In the meantime, Russian chemists discovered the spontaneous formation of complex shapes and permanently oscillating reactions (spontaneously arising from perfectly homogeneous solutions): Boris P. Belousov and Anatol M. Zhabotinsky¹⁰. The Russian-Belgian physical chemist Ilya Prigogine (1917-2003) later developed this whole domain of inquiry (labeled “dissipative structures”) into a high art, writing down the

⁹ Some of Turing’s statements in that paper sound rather preposterous today: “.... *it is only by courtesy that genes can be regarded as separate molecules. It would be more accurate (at any rate at mitosis) to regard them as radicals of the giant molecules known as chromosomes*”..... “*The function of genes is presumed to be purely catalytic. They catalyze the production of other morphogens, which in turn may only be catalysts.*”

¹⁰ An interesting anecdote: Belousov (Director of the Institute of Biophysics in Moscow) submitted a paper to a scientific journal purporting to have discovered an oscillating chemical reaction in 1951. It was roundly rejected with a critical note from the editor that it was clearly impossible. The editor’s confidence in its impossibility was such that even though the paper was accompanied by the relatively simple procedure for performing the reaction, he could not be troubled. If citric acid, acidified bromate and a ceric salt were mixed together the resulting solution oscillated periodically between yellow and clear. He had discovered a chemical oscillator. (See the website of Aliev R. Rubin Inst. Theoretical & Experimental Biophysics□Puschino, Moscow Region, Russia and movie clips of such reactions in <http://online.redwoods.cc.ca.us/instruct/darnold/DEProj/Sp98/Gabe/intro.htm>)

complete physical and chemical theory of these phenomena, down to quantum physics, (his 1977 Nobel lecture remains quite illuminating). Interestingly for us, a debate between Prigogine and Jacques Monod flared up, in which the role of natural selection versus the role of spontaneous morphogenesis was the cornerstone of the disagreement. Neglected or marginalized by Monod (just as it was by all his colleagues in molecular genetics) but touted by Prigogine, the importance of complex spontaneous morphogenesis in evolution had still to emerge into full view.

A prestigious ally of Prigogine's was the French mathematician René Thom (see Prigogine's Nobel lecture), who had been awarded the coveted (by mathematicians the world over) Fields Medal in 1958 for the theory of structural stability and morphogenesis. His universal classification of discontinuous morphogenetic forms into seven elementary "catastrophes" under even slight critical variations of the control parameters¹¹ prompted Thom to venture into possible (and quite unfortunate) applications well beyond biology (sociology, psychoanalysis, semantics etc.). The English translation of Thom's main synthetic treatise *Structural Stability and Morphogenesis* (French original 1972, English edition 1975) has, significantly, a foreword by Conrad Hal Waddington, who was in those years looked upon with some suspicion by mainstream geneticists and embryologists, though in recent years his early discoveries of the role of epigenetics have vindicated the importance of a lot of his data (see the previous chapter). He coined terms such as "canalization", "canalized selection", "chreod" and "homeorhesis" to capture the constraints by physical and geometric factors acting on embryology and evolution. He

¹¹ Catastrophes in systems with only one state variable:

The fold (1 control parameter)

The cusp (2 control parameters)

The swallowtail (3 control parameters)

The butterfly (4 control parameters)

Catastrophes in systems with two state variables

The hyperbolic umbilic (3 control parameters)

The elliptic umbilic (3 control parameters)

The parabolic umbilic (4 control parameters)

Thom proved that no classification can be made at all for systems with more than 4 control parameters.

was held in great suspicion by mainstream molecular geneticists in those years (approximately the Sixties and the Seventies).¹²

This brief history can be wrapped up by mentioning later contributions¹³, by Stuart Kauffman, Brian Goodwin, Lewis Wolpert, Antonio Lima-de-Faria, Antonio Garcia-Bellido among others¹⁴. Special mention needs to be made of the recurrent insistence on the significance of laws of form in biological evolution by the late Stephen Jay Gould and his colleague and co-author Richard C. Lewontin. This whole field has been widely ignored by entire generations of militant geneticists, “wet” molecular biologists and molecular embryologists¹⁵. The age of specificity, starting with the discovery of the structure of DNA by Crick and Watson in 1953, steered molecular biology away from these relatively generic approaches. Perhaps for that reason, no concrete problem in genetics or micro-biology has yet been solved by appeal to laws of form, though connections between these fields are proliferating. As we are going to see, in diverse quarters, somewhat episodically, there is a return of the laws of form into biology. It’s reasonable to expect more and more in the years to come. The phenomena that have been uncovered represent serious and diversified challenges to gradualistic adaptationism and neo-Darwinism.

¹² An exception is the attention to, and endorsement of, Waddington’s work expressed in the 1985 review by Maynard Smith, Burian, Kauffman, Wolpert et al (Maynard Smith, Burian et al. 2005)

¹³ Mostly, it has to be said, by stressing the importance of the laws of form for evolution and development rather than offering workable concrete models.

¹⁴ Maynard Smith and Savage (1956) stressed how the law of the lever requires that any uncompensated changes in the speed with which a limb can be moved will reduce the force that it can exert.

¹⁵ Eva Jablonka and Marion Lamb, in a 2005 book that explains very clearly most of the recent developments in evolutionary biology and rightly pleads for a radical reconsideration of evolutionary theory, completely ignore the issue about laws of form. Curiously, they stress the need for a “fourth dimension” in evolution, ignoring that West, Brown and Enquist in 1999 had introduced this very expression for a totally different aspect of evolution (the fractal law) (West, Brown and Enquist 1997; West Brown, et al. 1999); West, Woodruff, et al. 2002). (see also Piattelli-Palmarini 2008).

The “fourth dimension” of living systems

The body masses of living organisms vary between 10^{-13} grams (bacteria) to 10^8 grams (whales), that is, by 21 orders of magnitude. It’s interesting to see how other physico-chemical and biological properties and processes, and their ratios, scale with mass. How, for instance, surfaces and internal rates of transport, rates of cellular metabolism, whole organism metabolic rate, heartbeat, blood circulation time and overall lifespan scale with mass. These are, of course, all three dimensional systems, so it seems astounding that all the scaling factors, encompassing micro-organisms, plants and animals, are multiples of $1/4^{\text{th}}$, not of $1/3^{\text{rd}}$.¹⁶

The puzzle has been solved in collaborative work by physicists and biologists at Los Alamos, Santa Fe and Albuquerque. In essence, they have discovered a “fourth dimension” of biological systems. The explanation of the one-fourth scaling laws was found “*in the fractal-like architecture of the hierarchical branching vascular networks that distribute resources within organisms*”. (West, Brown and Enquist 1999, page 1677). Their papers reveal a remarkable convergence between the experimental values and the predicted ones (sometimes down to the third decimal), under this hypothesis of fractal-like architecture, for properties such as, for instance: radius, pressure and blood velocity in the aorta, cardiac frequency, number and density of capillaries, overall metabolic rate, and many more. Their mathematically detailed model (refined over the years) (West, Woodruff et al. 2002) takes into account biological data such as the 60 thousand miles of the entire circulatory system of a human body (capillaries notably included) and the fact that the diameter of capillaries is an invariant in the realm of vertebrates.

Guiding criteria have been the maximization of the inner and outer exchange surfaces, while minimizing distances of internal transport (thus maximizing the rates of transport). A passage in the 1999 paper (page 1679) deserves full quote:

“Unlike the genetic code, which has evolved only once in the history of life,

¹⁶ The natural general equation is of the form $Y = Y_0(M)^b$ where b is the scaling exponent, M the body mass, and Y_0 a normalization constant. It turns out that b is a simple multiple of $1/4$. For instance:

- Diameter of tree trunks and aortas $b = 3/8$ (therefore, for their cross section area $b = 3/4$)
- Rates of cellular metabolism and heart beat $b = -1/4$
- Blood circulation time and life span $b = 1/4$
- Whole organism metabolic rate $b = 3/4$

fractal-like distribution networks that confer an additional effective fourth dimension have originated many times. Examples include extensive surface areas of leaves, gills, lungs, guts, kidneys, chloroplasts, and mitochondria, the whole-organism branching architecture of trees, sponges, hydrozoans, and crinoids, and the treelike networks of diverse respiratory and circulatory systems. [...] Although living things occupy a three-dimensional space, their internal physiology and anatomy operate as if they were four-dimensional. Quarter-power scaling laws are perhaps as universal and as uniquely biological as the biochemical pathways of metabolism, the structure and function of the genetic code and the process of natural selection.” In the words of these authors, natural selection has “*exploited variations on this fractal theme to produce the incredible variety of biological form and function*”. But there were “*severe geometric and physical constraints on metabolic processes*”.

The conclusion here is inescapable, that the driving force for these invariant scaling laws cannot have been natural selection. It's inconceivable that so many different organisms, spanning different kingdoms and phyla, may have blindly “tried” all sorts of power laws and that only those that have by chance “discovered” the one-fourth power law reproduced and thrived. The maximization principles that have constrained such a bewildering variety of biological forms are of a physico-chemical and topological nature. Biochemical pathways, the genetic code, developmental pathways and (yes) natural selection cannot possibly have shaped these geometries. They had no “choice” (so to speak) but to *exploit* these constraints and be channeled by them.

The same kind of lesson comes from calculations, and data, in the domain of brain connectivity.

Non-genomic nativism

This expression has been coined by Christopher Cherniak and collaborators at the University of Maryland, ever since 1999. (Cherniak, Changizi et al. 1999; Cherniak, Mokhtarzada et al. 2004; Cherniak 2008, in press). Combining detailed anatomo-physiological analysis of the nervous system of the earthworm nematode, all the way up to the cortex of cats and monkeys, with a long series of computational simulations, it

emerged that the minimization of connection costs among interconnected components appears either perfect, or as good as can be detected with current methods. Such wiring minimization can be observed at various levels of nervous systems, invertebrate and vertebrate, from placement of the entire brain in the body down to the subcellular level of neuron arbor geometry. These instances of optimized neuroanatomy include candidates for some of the most complex biological structures known to be derivable "for free, directly from physics" (sic). Such a "Physics suffices" picture for some biological self-organization directs attention to innate structure via non-genomic mechanisms.

Since general network optimization problems are easy to state, but enormously computationally costly to solve exactly (they are in general what computer scientists call NP-hard, that is: exponentially exploding in complexity), some simplifications had to be introduced. A "formalism of scarcity" of interconnections (the so-called Steiner trees) was borrowed from engineering and used as the computational engine of network optimization theory, which characterizes efficient use of limited connection resources.¹⁷ Cherniak et al. conclude that the cortex is better designed than the best industrial micro-chip. For the macaque, fewer than one in a million of all alternative layouts conform to the adjacency rule better than the actual layout of the complete macaque set. In the relatively simpler case of the earthworm, the nematode (*Coenorhabditis elegans*) its nervous system having been the first ever to be fully mapped, the actual layout of 11 ganglia is the wirelength-minimizing one, out of 40 million alternative possibilities.

In a paper in print Cherniak specifies that:

“The neural optimization paradigm is a structuralist position, postulating innate abstract internal structure – as opposed to an empty-organism blank-slate account, without structure built into the hardware (structure is instead vacuumed up from input). The optimization account is thereby related to Continental rationalism; but for brain structure, rather than the more familiar mental structure”.

His message is that there is a "pre-formatting" issue for evolutionary theory. Seeing neuroanatomy so intimately meshed with the computational order of the Universe brings one back, as he suggests, to the explanatory project of D'Arcy Thompson and Turing.

¹⁷ The field matured in the 1970's for microcircuit design, typically to minimize the total length of wire needed to make a given set of connections among components.

(Cherniak 2008 (in print)). There is, indeed, in our terminology, a return of the laws of form.¹⁸

Some further examples are reported here. They all share the property that we have been emphasized: Evolution seems to have achieved near optimal answers to questions which, if pursued by the application of exogenous filters to solutions generated at random, as the neo-Darwinist model requires, would have imposed searching implausibly large of spaces of candidate solutions. This seems a hopeless enigma unless prior filtering by endogenous constraints are assumed.

Further instances of near optimal solutions to evolutionary `problems`.

- The brain's gray and white matter

The segregation of the brain into gray and white matter has been shown by biophysicists to be a natural consequence of minimizing conduction delay in a highly interconnected neuronal network. A model relating the optimal brain design to the basic parameters of the network, such as the numbers of neurons and connections between them, as well as wire diameters, makes testable predictions all of which are confirmed by anatomical data on the mammalian neocortex and neostriatum, the avian telencephalon, and the spinal cord in a variety of species (of mammals and birds). (Wen and Chklovskii 2005)

-Invariants of animal locomotion

Scaling laws and invariants in animal locomotion have been uncovered by the engineer Adrian Bejan (Duke University) and the biologist James H. Marden (UPenn) by considering that:

¹⁸ The nearly optimal character of the genetic code is another instance. Among thousands of possible alternatives, the genetic code as we know it is optimal for minimizing the effect of frame-shift mutations and minimizing the energy wasted in synthesizing the start of anomalous protein sequences. In the words of the authors: "*the universal genetic code can efficiently carry arbitrary parallel codes much better than the vast majority of other possible genetic codes*". (Itzkovitz & Alon, 2007).

“Animal locomotion is no different than other flows, animate and inanimate: they all develop (morph, evolve) architecture in space and time (self-organization, self-optimization), so that they optimize the flow of material.” (p. 246) (Bejan and Marden 2006).

Pulling together, in their model, “constructal” (sic) principles, equally applicable to the morphing of river basins, atmospheric circulation, the design of ships and submarines, and to animal locomotion, regardless of whether it consists in crawling, running, swimming or flying, they can explain the nature of the constraints and derive principles for optimized locomotion. The parameters that characterize, for each species, the locomotion that accomplishes the most for unit of energy consumed, i.e the points at the bottom of the U-shaped curve of cost versus speed, align neatly along a straight line in a logarithmic scale. Plotting optimal force against body mass, from the smallest marine creature to elephants, this straight line scales the very narrow range of speeds that maximize, for each species, the ratio of distance traveled to energy expended.

Simple equations that correlate body mass, body density, body length, the gravitational acceleration and the coefficient of friction, reveal that even the distinction between flying, swimming and walking (crawling, running) is immaterial. Physical principles of optimization and simple scaling laws govern the phenomena of animal locomotion.

- The physics of birdsong

Two physicists and a biologist, publishing in a physics journal, show that *“the respiratory patterns of the highly complex and variable temporal organization of song in the canary (Serinus canaria) can be generated as solutions of a simple model describing the integration between song control and respiratory centers. This example suggests that sub-harmonic behavior can play an important role in providing a complex variety of responses with minimal neural substrate”*. A straightforward generalization to other kinds of birdsongs in other species of singing birds is plausibly anticipated. (Trevisan, Mindlin et al. 2006)

We want to raise the issue: have all sorts of suboptimal neuronal setups and of the ensuing suboptimal singing patterns been tried out at random over the eons and natural

selection made it so that only the optimal singers left a descendance? Did the sub-harmonic equations become slowly, by chance trials and selection, become encoded in the canary genes? Or are we witnessing an instance of physical optimization constraints channeling genetic, developmental and behavioral traits?

-The perfect leaves

In the plant kingdom, a team of American and French biologists and physicists has recently determined by means of mathematical equations and artificially generated parallel channel networks in polymeric material layers, that the scaling relations for evaporatively driven flow through simple networks reveal basic design principles for the engineering of evaporation–permeation-driven devices. These authors highlight the role of physical constraints on the biological design of leaves (Noblin, Mahadevan, Coomaswami, Weitz, Holbrook and Zwieniecki 2008)¹⁹ They show that the flow rate through their bio-mimetic and real leaves increases linearly with channel density until the distance between channels is comparable with the thickness of the polymer layer, above which the flow rate saturates. A comparison with the plant vascular networks shows that the same optimization criterion can be used to describe the placement of veins in leaves.

- Optimal foraging strategies

As Von Fritsch had taught us, at the start of a foraging period, some individuals go out foraging on their own ('proactive' searchers) and some ('reactive' searchers) await information from returning foragers that is conveyed by the famous bee dance. The issue to be solved was: which percentage of individuals should go out and forage on their own and which percentage should wait for information (reactive searchers)? Clearly, it can't be the case that *all* searchers are reactive; so the question arises whether there is an optimal percentage of proactive to reactive searchers (as a function of colony size and the availability of perishable food). Researchers (Dechaume-Moncharmont, Dornhaus et al.

¹⁹ They say: "*The long evolution of vascular plants has resulted in a tremendous variety of natural networks responsible for the evaporatively driven transport of water. Nevertheless [until now] , little [wa]s known about the physical principles that constrain vascular architecture*". (page 9140)

2005) combined measurements of actual foraging behaviors with a mathematical model of the energy gain by a colony as a function both of the probability of finding food sources and of the duration of their availability. The key factor is the ratio of pro-active foragers to re-active foragers. Under specifiable conditions, the optimum strategy is totally independent (pro-active) foraging for all the bees, because potentially valuable information that re-active foragers may gain from successful foragers is not worth waiting for. This counter-intuitive outcome is remarkably robust over a wide range of parameters. It occurs because food sources are only available for a limited period. But their study emphasizes the importance of time constraints and the analysis of dynamics, not just steady states, to understand social insect foraging. The predictions of their model for optimal foraging, often quite counterintuitive, have been confirmed both in the wild and in laboratory conditions. (Dechaume-Moncharmont, Dornhaus et al. 2005). The bees appear to be “sitting” (so to speak) at the optimum of the curve of the possible ratios of proactive versus reactive foragers in a variety of situations.

Once again, we want to raise the issue: have all sorts of foraging strategies been tried out at random over the eons, and natural selection determined that only the optimal foraging bees left descendents? A progeny in which some kind of computation of the optimal ratio of proactive and reactive foragers became encoded in the genes? The question here involves multiple individuals and their behavior, and is more complex than that of the individual canaries. The issue needs to be raised nonetheless

We have seen examples where it seems that only physico-chemical and geometric constraints can explain the narrow canalizations that natural selection must have explored. The case of the bees, and two more that we are going to see (just a sample among many more in the recent literature) are such that the space of possible solutions to be explored seems too gigantic to have been explored by blind trial and error. The inference appears to be that a highly constrained search must have taken place. Accordingly, the role of natural selection may have been mostly just fine tuning. Or less.

- *The perfect wing-stroke*

The utility of one sixth or one fifth of a wing has been questioned for quite some time (including by one of us in past writing) as a challenge for gradualist adaptationism. A different tack is taken in a paper published in *Nature* in January 2008 by Kenneth P. Dial, Brandon E. Jackson and Paolo Segre. They present the first comparison of wing-stroke kinematics of the primary locomotor modes (descending flight and incline flap-running) that lead to level-flapping flight in juvenile ground birds throughout development. They offer results “*that are contrary both to popular perception and inferences from other studies*”. Prior to this study, no empirical data existed on wing-stroke dynamics in an experimental evolutionary context. In a nutshell, starting shortly after hatching and continuing through adulthood, ground birds use a wing-stroke confined to a narrow range of less than 20 degrees, when referenced to gravity, that directs aerodynamic forces about 40 degrees above horizontal, permitting a 180 degrees range in the direction of travel. Estimated force orientations from the birds’ conserved wing-stroke are limited to a narrow wedge. A main result of their extremely detailed comparative analysis of the wing-stroke plane angle, estimated force orientation and angle of attack among locomotor styles is that, when wingstroke plane angles are viewed side-by-side in both the vertebral and gravitational frames of reference, the wing-stroke is nearly invariant relative to gravity, whereas the body axis re-orientates among different modes of locomotion.

Their experimental observations reveal that birds move their ‘proto-wings’, and their fully developed wings, through a stereotypic or fundamental kinematic pathway so that they may flap–run over obstacles, control descending flight and ultimately perform level flapping flight. Interestingly, these authors offer the hypothesis:

“that the transitional stages leading to the evolution of avian flight correspond both behaviourally and morphologically to the transitional stages observed in ontogenetic forms. Specifically, from flightless hatchlings to flight-capable juveniles, many ground birds express a ‘transitional wing’ during development that is representative of evolutionary transitional forms”.

They say that locomotor abilities of extinct taxa, such as the recently discovered fossil forms possessing what is assumed to be ‘half a wing’, and long cursorial legs,

might be better understood if we evaluate how proto-wings and hindlimbs function during ontogeny in extant taxa. Their experimental observations show that proto-wings moving through a stereotypic and conserved wing-stroke have immediate aerodynamic function, and that transitioning to powered flapping flight is limited by the relative size of the wing and muscle power, rather than development of a complex repertoire of wing-beat kinematics.

Fine, but then, in our view, another problem arises for gradualistic adaptationism, because another kind of discontinuity is appealed to. In their own words:

“...the gravity based wing-stroke did not come about through a long series of migrational stages of the forelimb (from ventro-lateral to lateral to dorso-lateral): rather, the primitive wing-stroke started in a similar orientation as we see it today in hatchlings using their proto-wings”.

The angles of effective wing-stroke are extremely narrow, as these authors have determined, and one wants to question the process through which this narrow wedge of angles became fixated even before there was any real flight. The amplitude of the search space for the optimal angle seems to be even more daunting than that of the search space for the series of migrational stages (ventro-lateral to lateral to dorso-ventral). One cannot help wondering, in this case too, whether physical (gravitational, aerodynamic) constraints have not narrowed down the search space drastically. Evo-developmental mechanisms seem once more to have been severely constrained by non-biological and surely non-selectional factors.

- The zombifying wasp

Finally, a case (again, amongst many) in which the genetic programming of a complex behavior makes no doubt. Such behaviors can be shown to be completely automatic throughout the whole sequence, and un-learned. To cut a long story short, a particular species of wasps (*Ampulex compressa*) uses a venom cocktail to manipulate the behavior of its cockroach prey. As other species of wasps do too, the wasp paralyzes the cockroach without killing it, and then transports it into her nest and deposits her eggs into the belly of the cockroach, so that the hatchlings can feed on the cockroach's live body. What is peculiar to this species of wasps is that, by means of two consecutive stings,

separated by a rather precise time interval, in two different and precisely chosen parts of the cockroach nervous system, the wasp becomes capable of literally “driving” the zombified cockroach into her prepared nest. The wasp does not have to physically drag the cockroach into the pit, because it can manipulate the cockroach’s antennae, or literally ride on top of it, steering it as if it were a dog by a leash, or a horse by a bridle. (Liberat 2003). The first sting in the thorax causes a transient front leg paralysis lasting a few minutes. Some behaviors are blocked but not others. The second sting, several minutes after, is directly in the head.

As a result the wasp can grab one of the cockroach’s antennae and walk to a suitable oviposition location. The cockroach follows the wasp in a docile manner like a dog on a leash (Williams 1942; Fouad et al. 1994). A few days later, the cockroach serves as an immobilized and fresh food source for the wasp’s offspring.

Some evolutionary questions

This rather horrendous entomological saga suggests some key evolutionary questions. Such complex, sequential, rigidly pre-programmed, behavior could have gone wrong in many ways, at any one of its steps. The biochemical nature of the cocktail of venoms could have been different in many ways, being, as a result, either totally ineffective, or overdoing it, by killing the prey. The timing and location of the stings could have gone wrong in many ways, letting the cockroach recover, for instance, and kill the much smaller wasp. The wasp could have failed to “understand” that the prey can be led by the leash, after these two master strokes, and could have painfully dragged the rather big body to the nest. And so on and so on. The ways in which this behavioral sequence could have gone awry are indeed innumerable. Should we think that all kinds of alternatives have been blindly tried out by the ancestors of the wasp and that better and better solutions were progressively selected, and that this optimal solution was finally retained and encoded for in the genes? True: wasps have been around for a very long time (some 400 million years, maybe more) but even this is not a long enough time to try out innumerable alternative behavioral solutions, with alternative possibilities conceivable at each step of the behavioral sequence. What, then? No one knows at present. Such cases of elaborate innate behavioral programs (spider webs, bee foraging as we saw above, and

many more) cannot be accounted for by means of optimizing physico-chemical or geometric factors. But they can hardly be accounted for by gradualistic adaptation either. It's fair to acknowledge that, though we bet that some naturalistic explanation will one day be found, we have no such explanation at present. And if we insist that natural selection is the only way to try, we will never have one.

There is only so much that the 25,000 or so genes in the human genome *can* do to assemble a human being. *To be sure*, there are multiple gene regulations and networks of interactions, and morphogenetic attractors, and epigenetic modifications, and a complex interaction with an environment that, in the case of humans, comprises "culture". But this is far from being enough. Among other complex structures, tens of millions of kinds of antibodies have to be produced, and 10^{11} neurons and 10^{13} situated synapses to be developed and fixated, and about 60,000 miles of veins, arteries and capillaries to be exactly placed in each of our bodies. Cherniak's notion of "non-genomic nativism" is interesting and, it appears, inescapable.

Wrap-up of this chapter

Neo-Darwinists are keen to say that natural selection never optimizes, it only finds locally satisfactory solutions. From François Jacob's evolutionary "tinkering" to Maynard Smith's and Dennett's "satisficing"²⁰ emphasis is always put on this consideration. It is important to our critique of neo-Darwinism that the problem of finding *optimal* solutions to evolutionary problems by filtering candidates generated at random would often be intractable. But, as we have just seen, there *are* instances of optimal (or near-optimal) solutions to problems in biology; so, if natural selection cannot optimize something else must be involved. Very plausibly, the 'something else' includes: physics, chemistry,

²⁰ The term "satisficing", initially coined in the domain of decision-making by the economist and psychologist Herbert Simon (1916-2001), Nobel Prize for Economics 1978, characterizes a strategy which, somewhat more modestly and more rapidly, attempts to meet criteria for adequacy, rather than to identify an optimal solution. Under this or similar labels, the concept has been widely adopted by evolutionary biologists like John Maynard Smith, by neo-Darwinian cognitive scientists like Daniel Dennett and Gerd Gigerenzer (fast and frugal heuristics) and by researchers in artificial intelligence and computer science.

autocatalytic processes, dissipative structures and principles of self-organization, and surely other factors that the progress of science will in due time reveal.

The moral here is a sort of dilemma for neo-Darwinists: suppose, for the sake of argument, that natural selection does operate in the way that canonical neo-Darwinism claims it does, its degrees of freedom must be severely *restricted*. The minute proportion of the theoretical morpho-spaces of life that are actually occupied (McGhee 2007; Raup 1966) is something that the theory of natural selection cannot account for.²¹ We are understandably awed by the variety and the diversity of the forms of life, but it is important to underline that, at an abstract level, the extant and extinct forms of life are a very tiny subset of what is possible in the abstract.

As we just said, this dilemma would hold even if the theory of natural selection were otherwise basically correct. But the issue is arguably academic since the following chapters will show that it isn't.

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²¹ Evolutionary biology has traditionally been concerned with explaining why there are the life forms that there are. By contrast, the present issue is why there aren't the life forms that there aren't (see the previous chapter). We will return to such issues also in Chapter 8.

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