EVOLUTION

On the Origins of Novelty and Variation

Brian Charlesworth

In chapter 6 of *The Origin of Species*, Charles Darwin confronted the problem of explaining the evolution of complex pieces of biological machinery. How can natural selection, acting on "random" variation, produce a beautifully functioning structure made up of many integrated components, such as the vertebrate eye? His answer was that a structure like an eye is built up by a process of stepwise change from a primitive ancestral state, such as a simple group of light-receptive cells, leading eventually to the complicated vertebrate system of lens, iris, retina, optic nerve, etc. Each successive elaboration increases the efficiency of an already serviceable organ. Many such steps collectively produce a combination of characters that could never have existed in the ancestor. Although in the majority of cases we have no direct information on the steps that actually occurred in the evolution of complex adaptations, there are many examples of intermediate states that can be observed in living forms, as is indeed the case for the eye. The consensus among evolutionary biologists is that Darwin's interpretation has successfully stood the test of time, although the news has apparently not reached Kansas.

The Plausibility of Life
Resolving Darwin's Dilemma
by Marc W. Kirschner and John C. Gerhart
Yale University Press, New Haven, CT, 2005. 330 pp. $30, £18.95. ISBN 0-300-10865-6.

In *The Plausibility of Life*, an account intended for a general readership, Marc Kirschner and John Gerhart argue that the Darwinian explanation is incomplete and that the results of recent discoveries in cell and developmental biology can be used to remedy this defect. Are they right, or does their effort represent the latest entry in the catalogue of failed attempts by developmental biologists to supplement or replace neo-Darwinian evolutionary biology?

Unlike some of their predecessors, Kirschner (the chair of Harvard's Department of Systems Biology) and Gerhart (a professor in Berkeley's Department of Molecular and Cell Biology) are not hostile to the view that evolutionary change at the level of morphology or behavior is the product of natural selection acting on variation that arises ultimately from mutation. Rather, they argue that the basic properties of cells and their interactions during development have profound consequences for the properties of the variability available for use by selection. These properties and interactions both constrain the possible types of alteration to the organism's structures and offer opportunities for the rapid evolution of novel structures. The authors call the latter "facilitated variation," which they define as:

> An explanation of the organism's generation of complex phenotypic change from a small number of random changes of the genotype. We posit that the conserved components greatly facilitate evolutionary change by reducing the amount of genetic change required to generate phenotypic novelty, principally through their reuse in new combinations and in different parts of their adaptive ranges of performance.

Kirschner and Gerhart point out that development in multicellular animals is controlled by signal-response systems, in which many of the individual components are highly conserved over much of metazoan evolutionary history. The same molecules are often reused in different contexts; this "weak linkage" between signal and response permits conserved components to be combined in different contexts, allowing a novel outcome of development to be produced without the invention of new individual components. The authors also emphasize the flexibility of developmental systems, so that a change in the shape of a bone, for example, induces corresponding changes in the placement of blood vessels, nerves, etc., without requiring additional genetic changes. These points are illustrated with many impressive examples drawn from developmental and cell biology, subjects that are far better understood than when the modern synthesis of evolutionary biology was developed during the 1930s to 1950s. Perhaps the most striking example is the conservation of the basic genetic circuits underlying the body plans of animals as distant as vertebrates and arthropods, a great advance in our knowledge of the history of life.

The question is whether this adds substantially to our understanding of the causal processes of evolution. The authors' picture of the modern synthesis is rather a caricature. Early in their chapter on the sources of variation, they state "There are limits on what selection can accomplish. We must remember that it merely acts as a sieve, preserving some variants and rejecting others; it does not create variation. If genetic change were random, what could ensure that enough favorable phenotypic variation had taken place for selection to have produced the exquisite adaptations and variety we see on the earth today?" Near its end, they wonder "What if evolutionary biologists were wrong to think of phenotypic variation as random and unconstrained, even though genetic variation was random and unconstrained?"

There seem to be two mistakes here. First, the view of selection as a sieve ignores its ability to produce new combinations of characters, mentioned earlier. Such combinations give selection a truly creative aspect, as was strongly emphasized by Darwin himself and by many founders of the modern synthesis, whereas Kirschner and Gerhart focus on single mutational events. Second, the synthesis's founders were well aware of the fact that mutational effects are not unconstrained. For example, in 1947 H. J. Muller wrote that "the organism cannot be considered as infinitely plastic, and certainly not as equally plastic in all directions, since the directions which the effects of mutations can take are, of course, conditioned by the entire developmental and physiological systems arising from the action of all the other genes already present" (*1*).

Evidence of evolution's inventive powers.

It is very difficult, even now, to determine the potential range of variability in a given character, other than by examining the variability either produced by new mutations or present in natural populations. That is, of course, precisely what is done by evolutionary biologists interested in a particular trait. Until we have a predictive theory of developmental genetics, our understanding of the molecular basis of development—however fascinating and important in revealing the hidden history of what has happened in evolution—sheds lit-

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tle light on what variation is potentially available for the use of selection. As a result, it is currently impossible to evaluate the idea that developmental systems have special properties that facilitate variation useful for evolution. Indeed, Kirschner and Gerhart do not present any detailed examples of how the properties of developmental systems have actually contributed to the evolution of a major evolutionary novelty. Nor have they shown that alternative properties would have prevented such evolution. Although *The Plausibility of Life* contains many interesting facts and arguments, its major thesis is only weakly supported by the evidence.

Reference

1. H. J. Muller, in *Genetics, Paleontology, and Evolution*, G. L. Jepsen, G. G. Simpson, E. Mayr, Eds. (Princeton Univ. Press, Princeton, NJ, 1949).

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PHYSICS

Many Perspectives on Swinging

Alberto G. Rojo

In 1911, at the first Solvay Conference in Brussels, Albert Einstein and Hendrik A. Lorentz discussed a simple problem that later led to a central research tool within what we now call the "old quantum theory." At the time, it was assumed that mechanical systems subject to the yet embryonic quantum laws could only make "all or nothing jumps" between allowed states of different energy. What would happen, Lorentz asked, if one takes a pendulum with an allowed energy and shortens the length of the string by grasping it with two fingers? Einstein remarked that, even though the pendulum's period would decrease and its energy would increase, if the string is shortened very slowly ("adiabatically"), the product of the two quantities will remain constant: a pendulum whose frequency changes adiabatically does not undergo a quantum jump and the product of the period and frequency is quantized.

The Pendulum
A Case Study in Physics
by Gregory L. Baker and James A. Blackburn
Oxford University Press, Oxford, 2005. 300 pp. $89.50, £45. ISBN 0-19-856754-5.

This episode is just one of many notable instances in which the pendulum, the most famous of mechanical systems, surfaces in the history of physics. Our world abounds with examples of cyclic motions whose mathematical description is the same as that of the pendulum or coupled pendulums: Sound waves of well-defined frequency are oscillations of air pressure and velocity exactly analogous to the velocity of a pendulum at small displacements from its equilibrium position. Coupled microscopic magnets in a solid act as coupled pendulums and give rise to oscillations called magnons. Neutrino oscillations can be described as two coupled pendulums. And when humans walk, they do so as inverted pendulums. Given the ubiquity of this kind of periodic motions in physics, a book devoted thematically to the history and physics of the pendulum is most welcome.

The philosopher and the pendulum. Engraving from *L'Illustration* (Paris, 1851).

In *The Pendulum: A Case Study in Physics*, Gregory Baker and James Blackburn do an excellent job of weaving physical explanations with literary quotes and amusing anecdotes from the history of science. The authors are physicists who teach at Bryn Athyn College, Pennsylvania, and Wilfred Laurier University, Ontario, respectively, and they have written their account for undergraduate physics majors. After presenting simple examples of the linearized pendulum, the discussion turns to the nonlinear pendulum and parametric amplification with nice (although not fully self-contained) treatments of the pumping of a swing and O Botafumeiro, a giant censer at the cathedral of Santiago de Compostela in northwest Spain. (A team of men pull the supporting rope in a pumping cycle, thus transforming the censer's motion into that of a variable-length pendulum and increasing the system's energy and angle of oscillation.) A chapter devoted to the Foucault pendulum (which demonstrates Earth's rotation) combines the historical narration with a full treatment of the physical problem. The consideration of the torsion pendulum focuses on Henry Cavendish's 1798 experiment to measure the Newtonian gravitational constant *G* and Roland von Eötvös's results that established the equivalence of gravitational and inertial mass. The authors' presentation of the chaotic pendulum includes a good introduction to Poincaré sections and Lyapunov exponents.

The chapter on coupled pendulums could be used to introduce students to the physics of synchronization, a phenomenon that, as the authors explain, dates back to Christiaan Huygens and his observation of the synchronization of clocks hanging from the walls in his workshop. Baker and Blackburn offer a rather standard textbook treatment of the quantum mechanical harmonic oscillator and the Mathieu equation that describes the quantum mechanical simple pendulum. They next discuss superconductivity from the point of view of the macroscopic wave function and present Feynman's treatment of the Josephson junction using the algebra of coupled pendulums. The book culminates with an appealing treatment of the pendulum clock and Huygens's *Horologium Oscillatorium*, which includes a discussion of the escape mechanism in pendulum clocks, a topic not usually found in physics texts.

The book offers a tour of different incarnations of the pendulum, with nice interludes on Edgar Allan Poe's "The Pit and the Pendulum" (they don't reveal the end of the story) and "His Burial Too," Catherine Aird's mystery in which Foucault's pendulum is used as a murder weapon. In places, the mathematical treatments are incomplete and refer the reader to advanced texts. (Such is the case for the consideration of parametric forcing, which starts from the Lagrange formalism.) Although the book contains a good collection of end-of-chapter problems, it stands roughly midway between a monograph and an overview—with a slight emphasis on the encyclopedic rather than on new physical insights into well-known problems. As Baker and Blackburn state in the preface, *The Pendulum* is an unusual book. An enjoyable theme and variations, it is well suited for use as a resource or as a recommended text in an advanced course on mechanics.

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