

NEW BOOKS

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Lamarck Redux

Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life.

Eva Jablonka and Marion J. Lamb. MIT Press, Cambridge, MA, 2005. 472 pp. \$34.95 (ISBN 0262101076 cloth).

In the preface to the second edition of *Descent of Man* in 1874, Darwin remarked,

My critics frequently assume that I attribute all changes of corporeal structure and mental power exclusively to the natural selection of such variations as are often called spontaneous; whereas, even in the first edition of the 'Origin of Species,' I distinctly stated that great weight must be attributed to the inherited effects of use and disuse, with respect both to the body and mind.

In *The Variation of Animals and Plants under Domestication* in 1868, Darwin developed his pangenesis theory of heredity, whereby the gonads collect gemmules thrown off by all the tissues of the individual for transmission to the offspring in gametes. Such a system would easily support the inheritance of the effects of use and disuse. The conventional wisdom is that accepting the inheritance of acquired variation was Darwin's greatest error. Weismann's germ-soma distinction in the 1890s, and the rise of genetics, gradually undermined speculations about gemmules so that, by the period of the neo-Darwinian synthesis, the inheritance of acquired characters was thought to be defended only by the misguided and the eccentric. Eva Jablonka and Marion Lamb's latest book, *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life*, is a passionate and quite serious attempt to make the inheritance of acquired variation a central part of biology again.

The authors argue that four inheritance systems characterize biological systems. The first is the DNA-based genetic system. The second is the epigenetic inheritance system, whose role in the development of multicellular organisms has led to such wonderful molecular work in recent decades. The third is what they call the behavioral inheritance system, encompassing most forms of social learning in animals. Their fourth form is symbolic inheritance, exemplified by the human use of language to spread ideas. Each of these systems has a considerable number of subsystems. Epigenetic inheritance includes self-sustaining loops of gene activity, the transmission of variable cytoarchitectures, chromatin marking, and RNA silencing of genes. One could quibble with the four-part taxonomy, but it serves the purpose of the book well enough.

The existence of such a wide variety of inheritance systems will be an eye-opener for many biologists who have not had the opportunity to peruse work outside their own fields. I found the chapters on the genetic and epigenetic systems full of new and interesting information. Molecular biologists are likely to find the chapters on the behavioral and symbolic systems equally enlightening. Clear writing, illustrated with stories and quirky cartoons, makes the book a good read for any biologist.

But this book is not a simple recitation of interesting bits of recent biology. It is a hard-argued polemic for the importance of the inheritance of acquired variation across the whole spectrum of inheritance systems. If Jablonka and Lamb are correct, some form of inheritance of acquired variation is important in every organism. Some of these cases are uncontroversial. The behavioral and symbolic systems probably owe their adaptive properties to the fact that what one individual learns can be acquired by others via social learning. In one case that Jablonka and Lamb describe, a population of black rats exploits an Israeli pine plantation as if the rats were squirrels.

Some ancestral animal or animals discovered a technique for efficiently extracting seeds from pinecones. Now, in a considerable population of rats, the behavior is sustained by behavioral inheritance. Rat pups learn the technique by handling the partly opened cones their mother discards. Individual rats without such exposure have never learned the technique on their own in the laboratory. In the epigenetic inheritance system, cell lineages up-regulate some genes and silence others in response to signals received during embryogenesis. The chromosome marks that transmit this information do not alter DNA sequences, only gene activity. Epigenetically acquired variation is the fundamental mechanism by which the development of multicellular organisms takes place.

More controversially, does DNA inheritance exhibit the inheritance of acquired variation from generation to generation? Jablonka and Lamb are inclined to think that it commonly does. They argue that abundant evidence exists for contingent adaptive modification of the DNA inheritance system. Many species undergo facultative sexual reproduction in stressful environments. The mutation rates of bacteria, at least, seem to increase with stress. Pathogenic bacteria are hypermutable at loci that deal with the host's rapidly evolving immune system, even while other loci have normal rates of mutation. These features are not quite "instructed" evolution, but they verge on it. Mutation rates increase adaptively, but the direction of mutation is still blind with respect to adaptation.

In any single-celled creature, epigenetic changes will be transmitted to offspring, and some evidence suggests that the epigenetic inheritance systems that underlie the development of multicellular animals are derived from epigenetic systems that single-celled organisms used for the adaptive inheritance of acquired variation between generations. Multicellular organisms without the separation of the germ line from the soma early in development can likewise transmit acquired

variations across the generations. Plants do not exhibit early germ-line segregation and hence can transmit epigenetic variation from generation to generation. E. J. Steele's highly controversial idea that somatically selected immune system variants might somehow be spliced by viruses into the germ line is mentioned in passing, though Jablonka and Lamb do not defend its plausibility. Perhaps the Weismannian animals can afford to segregate the germ line because they mainly use behavior to deal with variable environments and can often use behavioral transmission in lieu of other Lamarckian systems.

The interaction of inheritance systems is another way in which "instructed" Lamarckian effects can influence the DNA inheritance system indirectly. This idea goes back to Weismann's original idea of germ-line segregation. Conwy Lloyd Morgan, James Mark Baldwin, and Henry Fairfield Osborn all independently discovered what has come to be known as the Baldwin effect in the mid-1890s, after Weismann's influence was felt but before the rediscovery of Mendel's laws launched genetics. The Baldwin effect reconciled the apparent inheritance of acquired variation with Weismann's doctrine of segregation of the germ line. In the mid-20th century, C. H. Waddington explicitly linked instructed effects to genes. Animals learn, and what they learn alters the selection pressures that bear on their genes. Any mechanism of phenotypic flexibility will do. For example, an animal introduced into a new habitat may use some form of phenotypic flexibility to survive and reproduce. In so doing, it exposes its genes to selection, which will tend to make traits originally acquired innate.

Organisms also modify their niches in many ways, leading to "niche construction," as John Odling-Smee and his colleagues call this effect. Selection will then adapt a species to the niche that it has constructed. Beaver dams and the aquatic adaptations of the beaver are an example. Social learning can do the same thing. Human symbolic culture leads to massive changes in our physical and social environment, and surely selection has favored genes adapted to such envi-

ronments. Genes and culture can be said to coevolve. Jablonka and Lamb illustrate the concept of gene-culture coevolution with the example of adult lactose absorption. In all other mammals and in most human populations, lactase synthesis in the gut ends after weaning. In European and African populations with a long history of dairying, lactase synthesis continues in most adults, allowing these populations to make efficient use of fluid milk.

Jablonka and Lamb go some way beyond current evidence in envisioning major roles for Lamarckian processes in evolution. For example, the hard evidence from experimental studies of non-human social learning indicates that behavioral transmission is present in many social species, but that most such systems support only the transmission of a few simple variants. To be sure, observers of animal behavior in the field typically report more, and more complex, social learning than experimentalists can replicate in the lab. Some time will pass before this gap is closed. Much of the evidence in support of Lamarckian processes is still fragmentary, and the final weighing of the evidence might find them to be of substantial importance only in special cases like human culture, and to be curiosities elsewhere.

Darwin's acceptance of the inheritance of acquired variation turned substantially on his acceptance of evidence from poor experiments. But he also had an adaptive intuition. Given that organisms have sophisticated systems for acquiring adaptive variation, why would selection favor writing off each generation's investment in adaptive acquired variation and force its offspring to repeat a costly course of phenotypic adaptation? Theoretical models of cultural evolution show that this intuition is cogent, given spatial and temporal variation that is autocorrelated on the generation-to-generation time scale. Skepticism about Lamarckian processes is warranted, but Jablonka and Lamb marshal enough evidence to make dogmatic claims of the absence of such processes equally deserving of skepticism. Where the weight of the evidence eventually comes down will be of great interest.

PETER J. RICHERRSON
(e-mail: pjricherson@ucdavis.edu) is
with the Department of Environmental
Science and Policy at the University of
California-Davis. His main research
interest is cultural evolution.
He is the author, with Robert Boyd,
of *Not by Genes Alone*, which is
reviewed below.

MEMETICS BY ANOTHER NAME?

Not by Genes Alone: How Culture Transformed Human Evolution. Peter J. Richerson and Robert Boyd. University of Chicago Press, Chicago, 2005. 332 pp. \$30.00 (ISBN 0226712842 cloth).

Why are Peter Richerson and Robert Boyd so against memes? This is the question that baffled me all the way through this excellent book. Writing in a much more accessible form than they have before, Richerson and Boyd lay out their case for the role of culture in shaping the human mind and behavior. They describe vivid examples, from the conflict between the Nuer and Dinka peoples in Sudan to the gift exchange systems of the !Kung San, and from altruism within and between groups to the persisting isolation of the Hutterites and Amish.

Richerson and Boyd's is a strong form of gene-culture coevolution theory that emphasises population-level thinking. They dub the prevailing approach in evolutionary psychology the "big mistake hypothesis" because of the way it deals with maladaptive human behavior. For example, humans eat too much sugary food, spend enormous amounts of resources on education and learning, and are very poor at converting wealth into grandchildren. All this is clearly maladaptive from the gene's-eye point of view—and the way theories explain maladaptation is critical.

Rather than being a big mistake, Richerson and Boyd argue, such behavior is an unavoidable by-product of cumulative cultural adaptation. They make a good case, based on their extensive modeling

studies, that imitation evolved because it helps people adapt rapidly in a wide variety of environments. Once it evolved, however, this meant that maladaptive ideas were let in—that is, ideas whose content helps them to spread even though they do not enhance the genetic fitness of their carriers. A modern example is the childless professional who succeeds culturally by spreading ideas to students, colleagues, or employees. Selection cannot eliminate such maladaptive variants because adaptive information is costly to evaluate—hence Richerson and Boyd's own theory, the “costly information hypothesis.”

This sounds like a memetic argument. The theories, practices, and behaviors of these childless professionals are all selfish memes that spread for their own benefit. So why don't Richerson and Boyd think of it that way? In fact, they do discuss memes, and they even use the phrase “selfish memes” a few times, but in the end they reject memetics.

The population approach, they say, does not imply that cultural evolution is analogous to genetic evolution; nor does it depend on “discrete, faithfully replicating, genelike bits of information.” I quite agree, but then, so would Dawkins and most other memeticists. In his 1976 book *The Selfish Gene*, Dawkins did not invent the term “meme” to be an analog of “gene” but rather to provide an example of another replicator, that is, another example of information that is copied with variation and selection. So, although there may be interesting analogies between genes and memes, this is not the point. The point is that both are replicators, which means that some analogies may be close, but others will not. That there are significant differences between genes and memes, and between cultural and genetic evolution, is not a valid argument against memetics.

Nor do replicators have to be “discrete, faithfully replicating, genelike bits of information.” Dawkins long ago pointed out that the copying fidelity of most memes is very low, there is often no right way of deciding where one meme begins and another ends, and most memes do not appear to be particulate—themes later taken up by both Dennett (1995)

and me (Blackmore 1999). This does not disqualify songs, stories, scientific theories, or technologies from being replicators; it simply means that these memes are rather poor-quality replicators—as we might expect from an evolutionary process that began only a few million years ago, at most.

Could it be that Richerson and Boyd are merely rejecting the word “meme” because of its popular connotations, when their theory is really equivalent to memetics? I have wondered about this for many years, because it is clear that along the spectrum of gene–culture coevolution theories, that of Boyd and Richerson has always been the closest to memetics; that is, they have come very close to treating their cultural variants as true replicators that evolve in their own way, and without being firmly held on the genetic “leash” postulated by E. O. Wilson. The answer depends on whether Richerson and Boyd think that cultural variants are replicators or not. In this book we have the answer, and it is “no.”

In a section entitled “Cultural Variants Are Not Replicators,” they repeat the false claim that copying must be perfect for a replicator to count as such, and explore interesting arguments about the many and varied mechanisms of cultural transmission. For them the peculiarities of biased transmission, behavioral attractors, and error-prone imitation are reasons to reject the idea of culture as a system of replicators, whereas for me memes are obviously information that is copied with variation and selection; the real question, then, becomes an empirical one. How high does the fidelity have to be for an evolutionary process to get off the ground? If human imitation is good enough, then we should be justified in treating memes as replicators, shouldn't we?

You may be wondering whether this is all just quibbling over words, but I think not. Richerson and Boyd's theory really is different from memetics and has correspondingly different implications for both our past and our future. Although Richerson and Boyd describe humans and our culture as being like obligate mutualists, they still maintain that “culture is on a leash, all right,” even if the dog

on the end is big and clever. This is because, for them, “culture is an adaptation.” In other words, culture was adaptive for human genes, it evolved for that reason, and it has persisted for that reason, in spite of including some maladaptive elements. In this respect, the authors fit Dawkins's complaint about his 1970s colleagues: “In the last analysis they wish always to go back to ‘biological advantage’” (Dawkins 1976, p. 193). This is, in the end, the fundamental difference—where the power lies.

According to memetic theory, memes are true replicators and have the same replicator power as genes. Culture is not an adaptation and never was. Rather, imitation was an adaptation that had unintended consequences: It let loose a new replicator—the behaviors, skills, and artifacts that people copied. These memes then began evolving for their own benefit, because that is what replicators do, creating a new process that would, as Dawkins emphasized, “in no necessary sense be subservient to the old” (Dawkins 1976, p. 194). Culture could have killed us all off. Indeed it is still possible that it killed off other species that tried the imitation experiment. We simply do not know enough about the evolution of our hominid relatives to be sure. It is certainly possible, and indeed quite likely, that it will kill us all off in the near future. And as for that future, Richerson and Boyd do not venture their predictions, but memetics predicts an ever increasing information explosion as memes proliferate along with ever better meme machines to replace the phones, faxes, computers, and World Wide Web of today.

Which theory is right? Both are testable; we will wait and see. Meanwhile this book provides an excellent account of Richerson and Boyd's theory, and is a must-read for anyone interested in gene–culture coevolution.

SUSAN BLACKMORE

(e-mail: susan.blackmore@blueyonder.co.uk) is a freelance writer, lecturer, and broadcaster, and a visiting lecturer at the University of the West of England, Bristol. Her research interests include memes, evolutionary theory, consciousness, and meditation.

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THE POLITICS OF SCIENCE

The Republican War on Science. Chris Mooney. Basic Books, New York, 2005. 342 pp. \$24.95 (ISBN 0465046754 cloth).

Chris Mooney is an engaging writer and meticulous journalist. The extraordinary claims he makes in *The Republican War on Science* are substantiated by 72 small-type pages of interview dates, references, citations, and other documentation. Daniel Smith, in the *New York Times Magazine* of 4 September 2005, asked, "Is the Bush administration anti-science? Or is it scientists critical of the president who have forgotten that science and politics don't mix?" Mooney's is an affirmative, forceful, and detailed answer to the first question. It is not only the George W. Bush administration that is antiscience but also other Republican presidents, notably Ronald Reagan, as well as the Republican Congress, going back to Newt Gingrich's 1994 Contract with America, which brought a Republican majority to the House of Representatives and, later, to the US Senate as well.

Mooney's indictment is shared by many scientists. According to Donald Kennedy, editor of *Science* and former president of Stanford University (quoted in the *Times* article cited above), there is a general perception that "scientific conclusions, reached either within agencies or by people outside the government, are being changed for political reasons by people who have not done the scientific work."

When Barry Goldwater ran for president in 1964, a conservative movement of right-wing anti-intellectualism pervaded his campaign against the New Deal (em-

bodied, in the perception of that movement, by Lyndon B. Johnson), blended with deep distrust of the elite media, the nation's leading universities, and the "Eastern establishment." Goldwater went down to defeat, but the ideological merger of pro-business conservatives, cultural traditionalists, and the Christian right that he brought together would ultimately achieve political victory. During the 1970s, a slew of new conservative activist organizations, such as the Heritage Foundation (in 1973) and the Conservative Caucus (in 1974), joined preexisting conservative action groups and think tanks, such as the American Enterprise Institute. The members of this alliance had mixed views, at best, of the Nixon administration, since the Nixon years brought *Roe v. Wade*, the ban on DDT, the Supreme Court's banning of school prayer, the end of funding for the supersonic transport program, and the appointment of the environmentalist Russell Train as administrator of the Environmental Protection Agency.

Matters changed with the election in 1980 of Ronald Reagan, who during his two terms as California governor (1967–1975) had gained the trust and support of the conservative movement, and who contributed much to its expansion and political strength. At least in part out of deference to religious conservatives, such as domestic policy adviser Gary Bauer, President Reagan failed to acknowledge and speak about the AIDS epidemic until 1987, and pronounced that the theory of evolution was flawed and therefore schools should teach the biblical story of creation as well. "The pro-industry mood at the start of the Reagan administration was intoxicating," writes Mooney (p. 39). James Watt and Anne Gorsuch, two staunch anti-environmentalists, were appointed as heads, respectively, of the Department of the Interior and the Environmental Protection Agency. The Reagan administration supported industry's complaints against environmental regulation (appointing a task force on "regulatory reform"), exploited scientific uncertainty to challenge the developing consensus that human industrial emissions cause acid rain, and launched the Strategic Defense

Initiative, the "Star Wars" program that Reagan proclaimed as his "dream." Early in the Reagan years, the *Chicago Tribune* published a "hit list," uncovered by Congress, of scientists who were described with epithets such as "a Nader on taxes" and "bleeding-heart liberal." (I was one of the 15 scientists on the hit list. My sin: "anti-business; get rid of him.")

In 1994 the Republican Party gained control of the House of Representatives for the first time in four decades, led by Newt Gingrich. There are two Gingriches: the one who "presided over an era of stunning congressional science abuse" (p. 49), and the Gingrich who holds a PhD in history, has taught environmental studies, has bolstered nanotechnology, and in May 2002 (after leaving Congress) recommended in testimony before the Senate that funding for the National Science Foundation be tripled.

The Gingrich Republicans dismantled Congress's Office of Technology Assessment and inaugurated the freewheeling politicization of scientific expertise in Congress, with "experts" drawn from industry's lobbyists and from ideologically committed think tanks like the Heritage Foundation. Rep. Dana Rohrabacher of California, who had derided concerns over global warming as "liberal claptrap," presided over a series of major hearings entitled "Scientific Integrity and Public Trust," covering three environmental issues: ozone depletion, climate changes, and dioxin risks. Adversarial proceedings pitted scientific outliers against mainstream scientists, so that members of Congress, rather than scientists, would judge at the end who was right. Robert Walker, chair of the House Science Committee, justified the proceedings: "Hearings are about trying to find out what the various points of view are" (p. 56). No one would argue against free speech and expressing diversity of opinions, but Walker failed to acknowledge that science is not a democracy, or a court's proceedings, where both sides should be equally represented. The conservative media came in support: Rush Limbaugh proclaimed that the scientific findings about the role of CFCs (chlorofluorocarbons) in ozone depletion are "balderdash" and "poppycock." A systematic effort to undermine

the scientific consensus goes now under the banner of “sound science,” shorthand for the notion that “anti-pollution laws have gone to extremes, spending huge amounts of money to protect people from minuscule risks” (p. 69). President George W. Bush has invoked “sound science” on issues ranging from climate change to arsenic in drinking water.

On 9 August 2001, George W. Bush, in his first televised address to the nation, made the claim that “more than sixty genetically diverse” embryonic stem cells existed at the time, “one of the most flagrant purely scientific deceptions ever perpetuated by a US president on the unsuspecting public” (p. 2), and limited federal funding to research with stem cell lines already in existence at that time, “a case study of how bad scientific information fuels bad policy” (p. 185). Three years later, on 8 August 2004, Tommy Thompson, Bush’s secretary of health and human services, made the shocking assertion that “before anyone can successfully argue that the existing federal stem-cell policy needs to be broadened, we must first exhaust the potential of the stem-cell

lines made available within the policy” (quoted on p. 188).

Members of the Bush administration and the Republican Congress have claimed that abortion causes mental illness and other negative health outcomes in women, notably breast cancer, even though a massive study of 1.5 million Danish women, published in the *New England Journal of Medicine* in 1997, discounted the abortion–breast cancer link. In 2002, following a letter from 28 pro-life members of Congress, the National Cancer Institute (NCI) removed an online fact sheet that discounted any association between abortion and breast cancer. Thereafter, the NCI in 2003 assembled a workshop of more than 100 experts who, with the exception of one antiabortion advocate, reaffirmed that abortion is not associated with an increase in breast cancer risk.

In its first three years, the Bush administration executed an unprecedented attack on scientific results, which included the “editing” or suppression of reports from panels of the National Academy of Sciences and other advisory bod-

ies concerning global climate change, missile defense, and other issues. A reaction from the scientific community was conveyed to the media in a press conference held by the Union of Concerned Scientists on 18 February 2004, where it was announced that 60 leading scientists, including 20 Nobel Laureates, had signed a statement denouncing the Bush administration “for misrepresenting and suppressing scientific information and tampering with the process by which scientific advice makes its way to government officials” (p. 224). Shortly thereafter, the document was signed by 48 Nobel Laureates, 62 National Medal of Science recipients, 135 members of the National Academy of Sciences, and thousands of others. (Full disclosure: I was an early signatory of the document.)

The epilogue of Mooney’s book is a call to political action and journalistic good sense: “Science-abusing corporations must be fought in the courts, science-abusing religious conservatives...must be fought in the schools, the educational system, and the public arenas” (p. 254). Reporters “need to understand better

how science abusers exploit the journalistic norm of 'balance' [by] demanding equal treatment for fringe and widely discredited views..., and should treat fringe scientific claims with considerable skepticism" (p. 253).

FRANCISCO J. AYALA
(e-mail: fjayala@uci.edu) is University Professor and the Donald Bren Professor of Biological Sciences and professor of philosophy at the University of California–Irvine. On 12 June 2002, he received from President George W. Bush the National Medal of Science; from 1994 to 2001, he was a member of President Bill Clinton's PCAST, the President's Committee of Advisors on Science and Technology.

NEW BOOKS

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