Book Reviews

Evolutionary Flatland

Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life
Eva Jablonka and Marion J. Lamb
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Jablonka and Lamb have written a splendid book, for a well-educated lay audience as well as for professional biologists, on what they refer to as the four dimensions of evolution. Their first dimension is genetic, i.e., information that is directly encoded by DNA nucleotides. For their second, third, and fourth dimensions of evolution, the authors focus on Lamarckian evolution of information that is encoded by epigenetic information systems (EIS), behavioral information systems (BIS), and symbolic information systems (SIS). They use the term epigenetic to describe a suite of molecular phenomena other than DNA, such as cytosine methylation, chromatin marks, RNA editing, mini-RNAs, and prions, as well as various self-sustaining loops. They use the term behavioral to describe actions taken by metazoans with nervous systems. Jablonka and Lamb force us to think more deeply about the mechanisms of evolution, even if we eventually do not agree with their assertions. That alone makes this book worth reading. There is nothing more productive than learning about interesting natural history, experimental work, and evolutionary theory from extremely well-informed authors, especially when you get visceral reactions to their assertions.

Jablonka and Lamb espouse a Lamarckian perspective. They state, "Strictly speaking, Lamarckian evolution requires that the induced and later assimilated phenotypes are *adaptive* to the conditions that elicited them" (p. 273; emphasis in original). They do not define neo-Lamarckian, which I would define as evolution in which induced changes are adaptive to conditions that are *not necessarily those* that induced the change. Lamarckian evolution is thus a special case of neo-Lamarckian evolution, which (as I argue below) is itself a special case of neo-Darwinian evolution. Jablonka and Lamb also equate Lamarckian evolution with soft inheritance and with evolutionary developmental biology (EvoDevo), although neither equivalence is universally accepted.

Jablonka and Lamb truly shine when discussing genetic and epigenetic inheritance. Their introductory chapter on epigenetic inheritance is an up-to-date tour de force, with their chapter on the interplay of genetic and epigenetic inheritance almost as good. At the end of each chapter, they engage in a dialogue with a devil's advocate. Their dialogue on genetic inheritance is brilliant, even if they do not reach the euphonious and metaphorical levels of Hofstadter's "Achilles and the Tortoise" (in Hofstadter 1979). Jablonka and Lamb proffer the most extensive theoretical discussion I have ever seen of mechanisms by which epigenetic signals can be transmitted from the soma to the germ line. At the same time, they truly understand the differences between animals and plants, especially with respect to soma and germ line.

Jablonka and Lamb attempt the noblest of feats in attempting to unify evolutionary biology under a single rubric, which for them is Lamarckian evolution. Parsimony makes theory more credible, and they have gone further than most to provide a parsimonious framework spanning genetic, epigenetic, behavioral, cultural, and symbolic inheritance systems. Kudos. However, in so doing, Jablonka and Lamb inadvertently seem to make the argument that all evolutionary biology can be united under the rubric of neo-Darwinian evolution! They state,

> Dobzhansky, in 1937, described evolution as, "a change in the genetic composition of populations." The genes he was thinking of were, at that time, entirely hypothetical units whose existence had been deduced from numerical data in breeding experiments. What a gene

was *chemically*, and what went on between the genotype and the phenotype, were entirely unknown. (page 29, emphasis added)

Yet throughout their book, Jablonka and Lamb state that what matters is not the chemical nature of genes. Instead, they consider the functional unit of inheritance to be information, regardless of its physical or chemical basis. Taking their argument to its logical conclusion, neo-Darwinian evolution therefore encompasses epigenetic, behavioral, cultural, and symbolic inheritance. This is implicit in the title of Rutherford and Henikoff's (2003) paper "Quantitative epigenetics." The neo-Darwinian framework was also explicitly brought into the realm of behavioral information systems by Moore et al.'s (1997) indirect genetic effects. Neo-Darwinian theory was developed by Wright, Fisher, and Haldane before Dobzhansky's seminal book (1937), at a time when leading geneticists such as Jack Schultz still believed that the information content of genes was encoded by proteins. Yet, quantitative genetics worked beautifully in 1937, and it still does today. With a more expanded, i.e., traditional quantitative-genetic definition of what is a gene, the epigenetic signals of chromatin marks and cytosine methylation constitute genotypes rather than phenotypes. The distinction between genetic and epigenetic becomes even more blurred if we focus on decomposability. Jablonka and Lamb claim that genetic phenomena are always decomposable, whereas epigenetic (always?) are not. However, heritable cytosine methylation can certainly be decomposable, whereas, by definition, epistatic effects between nucleotides contain nondecomposable parts. Jablonka and Lamb's arguments thereby strengthen the assertion that neo-Lamarckian evolution and thus Lamarckian evolution are simply special cases of neo-Darwinian evolution. As the authors admit on page 16, "Darwin's theory of natural selection is a very general theory; it is not tied to any particular mechanism of heredity or cause of variation."

The biggest problem with this book is that it is too anthropocentric. The authors portray a progression of evolutionary complexity from lowly plants, fungi, and protists to the next highest level of complexity, which is occupied by animals with nervous systems, i.e., are more complex by virtue of their ability to communicate. However, by their own definitions, even plants have behavioral information systems. Many plants use behavioral cues to attract pollinators, which thereby act as the channel for transmitting information in the form of pollen. Jablonka and Lamb place humans at the zenith of their evolutionary progression because only humans possess symbolic information systems. But does a symbolic inheritance system really make humans any more complex than a fly or a eusocial ant? The one evolutionary feature that separates humans from most other organisms is our extreme panmixia (making it surprising that Fisher did not like people more), and not our possession of behavior or symbols.

The figures in this book virtually all contain anthropomorphized objects, such as molecules and other inanimate objects with faces, and often also arms and legs. Animals are depicted in human attire, often in a sexist fashion.

In at least one prominent instance the anthropomorphic images border on the political. Environmental factors are depicted by a bomb with a human face. This is an odd depiction insofar as evolutionary biologists often think of environmental factors as much more subtle, such as temperature changes. My initial reaction was that the authors consider a suicide bomber to be the prototypical environmental shock; a modern incarnation of Tennyson's "red in tooth and claw." However, there may be a logical political reason for this draconian depiction of environmental factors. Although often it is political suicide to mention such things, many biologists understand that the two biggest modern environmental problems are human population explosion and military escalation. My hat is off to the authors if this was their intent.

There are two facets to theory: (1) devising models that describe existing phenomena and (2) otherwise unexpected predictions from those models. For example, Einstein's theory of relativity gained credibility by his prediction and subsequent empirical corroboration regarding the orbit of Mercury. Similarly, biological theory should be more than just descriptive models and Kiplingesque just-so-stories, but instead be infused with bold, testable, and often outlandish predictions. Such predictions allow one to tease apart a given theory from most others. Jablonka and Lamb did a gorgeous job with the first facet of theory. However, they hardly treaded on the second facet of devising bold predictions arising from Lamarckian evolution that could be used to falsify their theory. Such bold predictions would have increased the length of the book and made it seem less authoritative to a lay audience. But, I do wish they had stuck their necks out. This book provided a great opportunity for such authoritative temerity.

Jablonka and Lamb's book raises many fascinating questions. For example, given that we have a nested sequence from Lamarckian to neo-Lamarckian to neo-Darwinian evolution, what are the relative contributions of each to total additive genetic variance? Likewise, given that we have four dimensions of heritable information carrying mechanisms—genetic, epigenetic, behavioral, and symbolic, regardless of whether these are Lamarckian, neo-Lamarckian and/or neo-Darwinian—what is the relative contribution of each to additive genetic variance? Despite the authors' reluctant protests, this would allow us to gauge whether the phenomena that Jablonka and Lamb highlight are major influences on evolutionary trajectories or just negligible tweaks. Unfortunately, sufficient data do not yet exist to answer these questions.

At a minimum, I would highly recommend this book to any incoming graduate students in evolutionary theory. Jablonka and Lamb show that you can do fascinating evolutionary theory without mathematics, something that is often forgotten in the wake of quantitative genetics and evolutionary game theory.

This book will often make your blood boil. However, in so doing, it will almost certainly get you to think of (1) ways to test their arguments, (2) possible logical inconsistencies in their arguments, (3) mathematical formalizations of their theories, (4) alternative theories, (5) the evolutionary implications of both their and alternative theories, and (6) further syntheses of evolutionary theories. One mark of a good book is how much it spurs on research by others. By that standard, Jablonka and Lamb seem to have done a superb job. Whether you agree with Jablonka and Lamb or not, *Evolution in Four Dimensions* is worthwhile reading for any evolutionary biologist.

References

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What's New?

Animal Innovation

Simon M. Reader and Kevin N. Laland, eds
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Japanese macaques washing sweet potatoes and blue tits opening milk bottles to drink the cream—to cite two well-known examples—are displaying innovative behaviors, "behavior patterns not previously found in the population," to quote Reader and Laland's definition in their thoughtful introduction to this book (p. 9). But there is a little more to innovation than simply doing something new for the species or population. A macaque that accidentally drops a potato into the water and then retrieves and eats it is not innovating. But if the macaque persists in dropping potatoes into water before eating them, then it is innovating. Innovation need not spread beyond one individual. Whether it does is a function of social learning opportunities and mechanisms available in the population. Nevertheless, the current wave of interest in animal social learning is undoubtedly at least partly impelled by the role innovation is assumed to play in originating animal "cultures" as are now so well much discussed chimpanzees (and here in chapters by Byrne, Galef, and Kummer and Goodall).

Attempts to study animal innovation experimentally date back at least to Klopfer's work with birds in the 1960s, as documented in Lefebvre and Bolhuis's chapter. However, current interest in it dates from the work of Lefebvre and colleagues which began to appear about ten years ago. From large numbers of more or less anecdotal reports of innovative behaviors in birds, analyzed in a way that controlled for such things as likelihood of observing or reporting on each species in the first place, they showed that innovation is distributed nonrandomly across species and that the tendency to innovate is related positively to overall brain size and to size of the neostriatum relative to the rest of the brain. Comparable relationships were then reported for primates, as detailed in Reader and MacDonald's and Sol's chapters in this book. The tendency to innovate may also, unsurprisingly perhaps, be related to the ability of a species to invade new habitats. Thus innovative tendency is potentially evolutionarily important.

But as with many labels for animal behavior borrowed from human behavior, what exactly is being labeled is rather slippery. Innovation is both a product—a persisting novel behavior in an individual or group—and the process that gives rise to it. Clearly, however, there must be more than one process. Innovations that do spread presumably do so by normal processes of social learning, of which there are many, and none of them is likely to be specific to behaviors classified by researchers as innovative. But is there any process unique to the generation of innovative behavior? Most of what is reported here, for example by Laland and van Bergen on guppies and Greenberg on birds, indicates not. Rather, as common sense suggests, innovative behavior arises from a concatenation of processes, and this could account for its occurrence being related positively to overall brain size. For example, to do something new, especially if that requires interacting with a new object, food, or location, it may help to be not too neophobic (Greenberg). To profit from a chance encounter with a new way of getting food, it helps to be hungry and to be able to learn quickly, not to mention that hunger may increase activity and thereby encounters with alternative food sources (Laland and van Bergen). It also helps not to have the usual food sources available. This may go to show that just as with people, "necessity is the mother of invention," but it is just as well an instance of a basic fact about instrumental conditioning with food: when reward is discontinued, i.e., in extinction, behavior becomes more variable. All of which goes