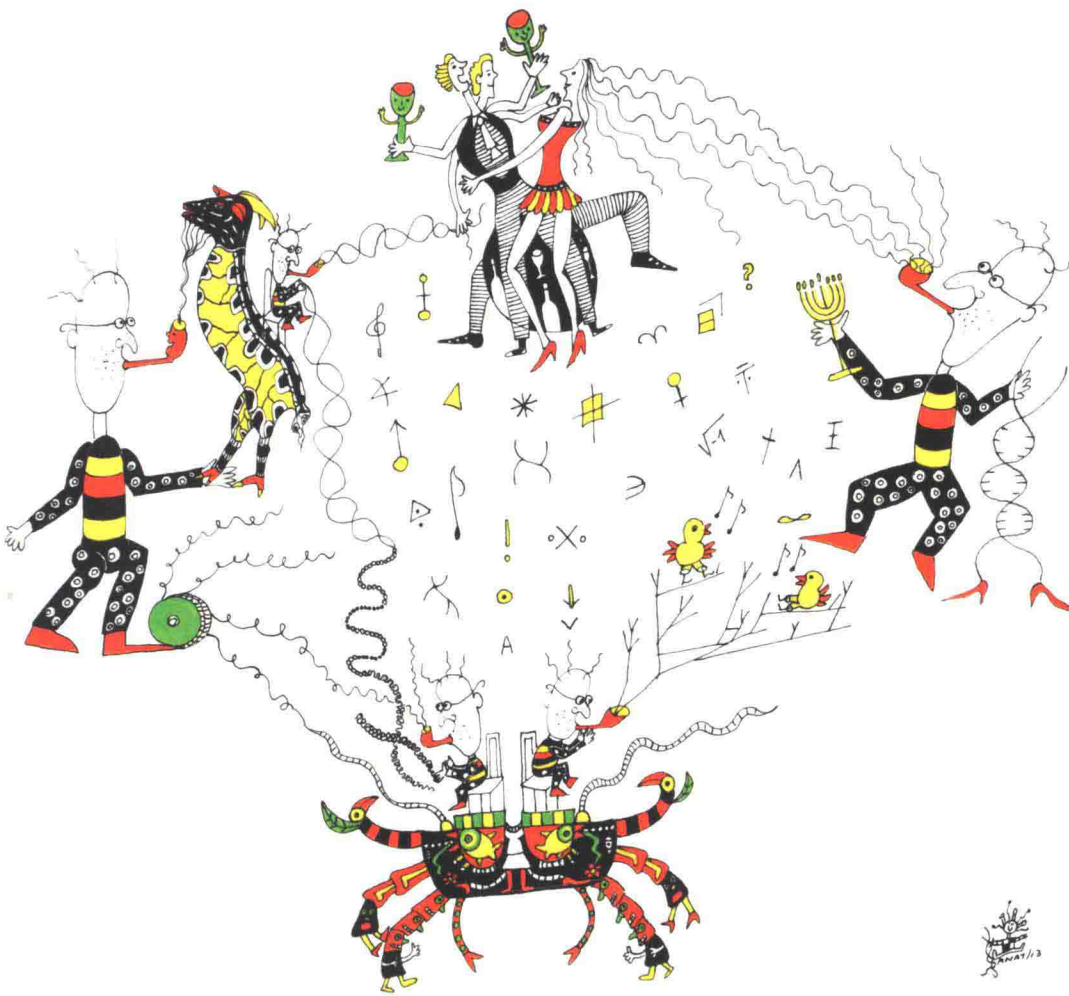
Evolution in Four Dimensions

Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life

va Jablonka and Marion J. Lamb

ustrated by Anna Zeligowski

revised edition



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Cooperation and Its Evolution, Volume 1: Agents and Environments, Kim Sterelny, Richard Joyce, Brett Calcott, and Ben Fraser, editors, 2012

Cooperation and Its Evolution, Volume 2: Agents and Mechanisms, Kim Sterelny, Richard Joyce, Brett Calcott, and Ben Fraser, editors, 2012

Ingenious Genes: How Gene Regulation Networks Evolve to Control Development, Roger Sansom, 2011

Yuck! The Nature and Moral Significance of Disgust, Daniel Kelly, 2011

Laws, Mind, and Free Will, Steven Horst, 2011

Perplexities of Consciousness, Eric Switzgebel, 2011

Humanity's End: Why We Should Reject Radical Enhancement, Nicholas Agar, 2010

Color Ontology and Color Science, Jonathan Cohen and Mohan Matthen, editors, 2010

The Extended Mind, Richard Menary, editor, 2010

To our genetic, epigenetic, and cultural parents and offspring

Preface to the Revised Edition

Since *Evolution in Four Dimensions* was first published, there has been a spate of new and exciting discoveries in biology. Many of the new findings are directly relevant to the topics we discussed in 2005, by and large supporting and often strengthening the arguments we put forward then. In addition to new facts, new ideas about evolution have also emerged; biologists have been questioning the assumptions on which twentieth-century evolutionary theory was based, and have proposed alternative ways of approaching evolutionary problems. In this edition of *E4D*, we introduce some of the new knowledge and fresh ideas, in the firm belief that they add weight to our view that the old, gene-based, Modern Synthesis version of evolutionary theory is inadequate for the twenty-first century.

We have left parts I to III of the book almost unchanged from the original edition, making only a few minor corrections, mainly typographical. For the benefit of ebook readers, we have also numbered all the endnotes chapter by chapter, and included markers for them in the text. Most of the new material is to be found in part IV, which is a single, long, additional chapter. To carry the reader through this we have made use of the dialogue form employed elsewhere in the book, with our interrogator (IM) asking us (ME) questions and questioning the answers we give. The chapter has five sections; in the first four, we go through each of our dimensions—the genetic, the epigenetic, the behavioral, and the symbolic—reviewing and updating the ideas and facts presented earlier. We devote quite a lot of space to the involvement of epigenetics in the other dimensions of heredity, because there has been an explosion of information in this area, which is both empirically and conceptually groundbreaking for evolutionary theory. In the fifth section of the chapter, we look at the general implications of the work we have been describing for ideas about evolution.

At the beginning of the endnotes for each chapter, we have added a short "nine years later" paragraph, in which we signpost where in the literature recent information is to be found. Many references have been added to the reference list, and there are additional entries in the index. With the help of Anna Zeligowski's drawings, we have tried to present the new material in a way that retains the spirit of the original edition of *E4D* and enhances its usefulness.

Acknowledgments

This book would not have been written without the encouragement and help of our friends, families, students and colleagues. We are grateful to all of them.

Part of the book was written while E. J. was a visitor at the Museum of Vertebrate Zoology, Berkeley, University of California, and we would like to thank David and Marvalee Wake and their colleagues for the good working environment they provided, and Martha Breed and the WW group for their company and the wonderful nature trips. We also want to thank everyone working at the Cohn Institute for the History and Philosophy of Science and Ideas at Tel Aviv University for their help and support. Our debt to the students in the Cohn Institute and the participants in the "Networks in Evolution" seminar at the European Forum Alpbach 2002 is a big one. Their comments and criticisms made us clarify many of our ideas and arguments, abandon some of them, and think deeply about how we should present the material in this book. We hope that they will enjoy the final product.

We have benefited from information and advice from many people, but our special thanks must go to those who have read and commented on various drafts of the book. Eytan Avital, Daniel Dor, Fanny Doljanski, Yehuda Elkana, Yehudit Elkana, Evelyn Fox Keller, James Griesemer, Revital Katznelson, Jawed Iqbal, Lia Nirgad, Christine Queitsch, Richard Strohman, Iddo Tavory, and Alan Templeton each read sections or chapters, and pointed out some of the errors and ambiguities in what we had written. Our long-suffering friends Lia Ettinger, Simona Ginsburg, and Joy Hoffman read drafts of the whole book, and their comments, criticism, and many valuable suggestions have made it a far better book than it would otherwise have been. Tom Stone, Philip Laughlin and their colleagues at the MIT Press were helpful and encouraging throughout, and we thank them for their guidance and excellent editorial work.

We also want to thank Rami of the Ha'Shloshah restaurant in Jerusalem. His hamousta soup sustained us through many long days, and many problems were resolved at his tables.

Finally we need to acknowledge the contribution of Beauty-the-cat, who sat on every page of the manuscript, thereby delaying its completion by several weeks. As an ex-feral cat, she was a constant reminder of the power of learning, active niche construction, and the coevolution of humans and cats.

Contents

Prologue

The content and format of this book are a little unusual, so we want to begin by explaining what it is about and how it is organized. Our basic claim is that biological thinking about heredity and evolution is undergoing a revolutionary change. What is emerging is a new synthesis, which challenges the gene-centered version of neo-Darwinism that has dominated biological thought for the last fifty years.

The conceptual changes that are taking place are based on knowledge from almost all branches of biology, but our focus in this book will be on heredity. We will be arguing that

- there is more to heredity than genes;
- some hereditary variations are nonrandom in origin;
- some acquired information is inherited;
- evolutionary change can result from instruction as well as selection.

These statements may sound heretical to anyone who has been taught the usual version of Darwin's theory of evolution, which is that adaptation occurs through natural selection of chance genetic variations. Nevertheless, they are firmly grounded on new data as well as on new ideas. Molecular biology has shown that many of the old assumptions about the genetic system, which is the basis of present-day neo-Darwinian theory, are incorrect. It has also shown that cells can transmit information to daughter cells through non-DNA (epigenetic) inheritance. This means that all organisms have at least two systems of heredity. In addition, many animals transmit information to others by behavioral means, which gives them a third heredity system. And we humans have a fourth, because symbol-based inheritance, particularly language, plays a substantial role in our evolution. It is therefore quite wrong to think about heredity and evolution solely in terms of the genetic system. Epigenetic, behavioral, and symbolic inheritance also provide variation on which natural selection can act.

When all four inheritance systems and the interactions between them are taken into account, a very different view of Darwinian evolution emerges. It is a view that may relieve the frustration that many people feel with the prevalent gene-centered approach, because it is no longer necessary to attribute the adaptive evolution of every biological structure and activity, including human behavior, to the selection of chance genetic variations that are blind to function. When all types of hereditary variation are considered, it becomes clear that induced and acquired changes also play a role in evolution. By adopting a four-dimensional perspective, it is possible to construct a far richer and more sophisticated theory of evolution, where the gene is not the sole focus of natural selection.

We have divided the book into three parts, each of which has a short introduction. Part I is devoted to the first dimension of heredity and evolution, the genetic system. In chapter 1 we outline the history of Darwin's theory and show how it became so gene-centered. Chapter 2 describes how molecular biology has changed the way biologists see the relation between genes and characters. In chapter 3 we examine the evidence suggesting that not all genetic changes should be seen as random, chance events.

Part II deals with the other dimensions of heredity. Chapter 4 is about the second dimension, epigenetic inheritance, through which different cells with identical DNA are able to transmit their characteristics to daughter cells. In chapter 5 we explore the ways in which animals transmit their behavior and preferences through social learning, which is the third dimension. We deal with the fourth dimension in chapter 6, which describes how information is transmitted through language and other forms of symbolic communication.

In part III of the book we put Humpty Dumpty together again. Having looked at each of the four dimensions of heredity more or less in isolation, we bring them together by showing how, in the long term, the systems of inheritance depend on each other and interact (chapters 7 and 8). In chapter 9 we discuss how they may have originated and how they have guided evolutionary history. Finally, in chapter 10, we summarize our position and put it into a wider perspective by considering some of the philosophical implications of the four-dimensional view, as well as some political and ethical issues.

Each chapter ends with a "dialogue," and the whole of chapter 10 takes this form. We use these dialogues as a device to enable us to reiterate some of the tricky points in our arguments, and to highlight areas of uncertainty and issues that are contentious. The participants in the dialogues are M.E. (who represents the authors, Marion Lamb and Eva Jablonka) and someone

Ipcha Mistabra

who could have been called the devil's advocate, but who, in order to avoid the negative connotations of that term, we have chosen to call Ipcha Mistabra (I.M. for short). *Ipcha Mistabra* is Aramaic for "the opposite conjecture." It is a term that embodies the argumentative dialogue style used in the Talmud, in which arguments are countered and contradicted, and through this dialectic a better understanding of the subject is reached. The book can be read without the dialogues, but we think that readers may find them interesting and helpful, because they reflect many of the questions and concerns that our students and others have raised when we have spoken about our evolutionary views.

We hope that the book can be read not only by professional scientists but also by the many people who are interested in biological ideas, and are fascinated (and sometimes worried) by the current ways of thinking about biology, especially about modern genetics. To make it as reader-friendly as possible without compromising the science, we have relegated the more specialized material and the sources of information to endnotes. We use many examples and thought experiments to try to make our ideas clear, but we recognize that some chapters (particularly chapters 3, 4, and 7) may be a bit heavy going for nonbiologists. These chapters include quite a lot of molecular detail, which we need in order to make our case to skeptical biologists. Readers who do not wish to delve into the molecular nitty-gritty can skip the more technical parts of these chapters, and read the general

discussions, although if they do so they will have to trust our intellectual honesty and judgment, rather than evaluate the data for themselves.

The book is intended to be both a synthesis and a challenge. It is a synthesis of the ideas about heredity that have come from recent studies in molecular and developmental biology, animal behavior, and cultural evolution. The challenge it offers is not to Darwin's theory of evolution through natural selection, but to the prevalent gene-based unidimensional version of it. There are four dimensions to heredity, and we should not ignore three of them. All four have to be considered if we are to attain a more complete understanding of evolution.

I The First Dimension

The first dimension of heredity and evolution is the genetic dimension. It is the fundamental system of information transfer in the biological world, and is central to the evolution of life on earth. For a century now, the genetic system has been studied intensely, and these studies have yielded rich dividends. Not only have they helped us to understand the natural world, they have also had significant practical effects in medicine and agriculture.

In the mid-twentieth century it became clear that the molecular basis of genetics was to be found in DNA and its replication, and from the mid-1970s, when genetic engineering got underway, knowledge about genetics began to expand at an unprecedented rate. With new technologies being invented almost daily, it was apparent by the early 1990s that the full DNA sequence of the human genome would soon be known. Molecular biologists were talking with prophetic certainty about the "book of life," which they would soon be reading; about the newly discovered "philosopher's stone"; about the Holy Grail they were uncovering. All of these metaphors referred to the sequencing of the human genome. Once the genome was sequenced, it was claimed, geneticists would be able to use the data to discover the hereditary weaknesses and strengths of an individual, and, where appropriate, benevolently intervene. Never before had biological knowledge seemed so powerful and so full of promise. And as the winter of 2001 drew to a close, the climax was at last reached—the draft sequence of the human genome was published. About 35,000 human genes (the number was later revised), scattered patchily on the twenty-three pairs of human chromosomes, had been identified, sequenced, and their locations made known. Newspapers were full of excited prophecies of a braver and healthier new world.

But the geneticists themselves, now in possession of the draft of the coveted "book of life," have shown a curious and almost schizophrenic response. On the one hand the excitement and sense of achievement are

so overwhelming that prophecies about the newly revealed promised land have been even more daring. On the other hand there is a new sense of humility. And ironically, it is the achievements of molecular biology that are causing the humility. The discoveries that are being made show how enormously complicated everything is. Just as in an earlier century, when the telescope opened up new horizons for astronomers and the microscope revealed new worlds to biologists, the revelations of molecular biology cannot be neatly slotted into the existing framework of thought. They do not make the old genetics more complete; rather, they highlight the simplifying assumptions that have been made and reveal vast areas of unanticipated complexity. Genes and genetics can no longer be looked at in quite the same way as in the past.

One of the things that molecular studies have reinforced is something that had already been accepted by modern geneticists: the popular conception of the gene as a simple causal agent is not valid. The idea that there is a gene *for* adventurousness, heart disease, obesity, religiosity, homosexuality, shyness, stupidity, or any other aspect of mind or body has no place on the platform of genetic discourse. Although many psychiatrists, biochemists, and other scientists *who are not geneticists* (yet express themselves with remarkable facility on genetic issues) still use the language of genes as simple causal agents, and promise their audience rapid solutions to all sorts of problems, they are no more than propagandists whose knowledge or motives must be suspect. The geneticists themselves now think and talk (most of the time) in terms of genetic networks composed of tens or hundreds of genes and gene products, which interact with each other and together affect the development of a particular trait. They recognize that whether or not a trait (a sexual preference, for example) develops does not depend, in the majority of cases, on a difference in a single gene. It involves interactions among many genes, many proteins and other types of molecule, and the environment in which an individual develops. For the foreseeable future, predicting what a collection of interacting genes will produce in a certain set of circumstances is not going to be possible. But despite this awareness, the sense of power generated by the success of the genome project has often masked caution, sometimes creating great and unrealistic hopes, and great and unrealistic fears.

The contagious reactions of excited scientists and business people are fascinating and important, because they will influence where time and money are invested in the future, but in what follows we are going to focus on the more direct consequences of the molecular discoveries of the last two decades of the twentieth century. Not only have they made people