

Modularity in Animal Development and Evolution: Elements of a Conceptual Framework for EvoDevo

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ABSTRACT For at least a century biologists have been talking, mostly in a black-box sense, about developmental mechanisms. Only recently have biologists succeeded broadly in fishing out the contents of these black boxes. Unfortunately the view from inside the black box is almost as obscure as that from without, and developmental biologists increasingly confront the need to synthesize known facts about developmental phenomena into mechanistic descriptions of complex systems. To evolutionary biologists, the emerging understanding of developmental mechanisms is an opportunity to understand the origins of variation not just in the selective milieu but also in the variability of the developmental process, the substrate for morphological change. Ultimately, evolutionary developmental biology (EvoDevo) expects to articulate how the diversity of organic form results from adaptive variation in development. This ambition demands a shift in the way biologists describe causality, and the central problem of EvoDevo is to understand how the architecture of development confers evolvability. We argue in this essay that it makes little sense to think of this question in terms of individual gene function or isolated morphometrics, but rather in terms of higher-order modules such as gene networks and homologous characters. We outline the conceptual challenges raised by this shift in perspective, then present a selection of case studies we believe to be paradigmatic for how biologists think about modularity in development and evolution. *J. Exp. Zool. (Mol. Dev. Evol.)* 285:307-325, 1999. © 1999 Wiley-Liss, Inc.

Biologists have long recognized that the evolvability of development is the key to morphological evolution. However, only recently has molecular genetics produced substantial characterizations of developmental regulatory processes and thus made it possible to analyze them comparatively. This has fueled resurgent interest in the evolution of development, but evolutionary developmental biology (EvoDevo) lacks a clear conceptual framework. Blithe attempts to apply classical comparative concepts to development lead more often than not to confusing or contradictory results. Furthermore the idea that one should focus on developmental mechanisms as units of evolutionary change begs the question, what constitutes a developmental mechanism?¹

Classical accounts of animal form concentrate on identifying morphological characters and on tracing their phylogenetic modification. The dichotomous notions of homology and analogy are implicitly predicated on a modular view of animal design; their ease of use is proportional to the ease with which one can identify the modules. Embryogenesis, too, consists of logically separable processes—gastrulation, establishment of body axes or morphogenesis of individual organs or appendages—and we take

for granted that logical separability reflects underlying modularity: the experimental study of development assumes that one may meaningfully isolate (physically or conceptually) and study individual processes independent from one another. Functional decomposability is thus a necessary presumption to considering developmental mechanisms either as units of explanation within de-

¹This essay arose from a workshop on modularity in development and evolution organized by the authors and Dr. Evelyn Fox Keller, held in September 1997 at the Friday Harbor Laboratories. In addition to the authors, the participants were Drs. Jessica Bolker, Richard Huxian, Marie-Anne Félix, Scott Gilbert, Jason Hodin, Evelyn Fox Keller, Eli Moeir, Jay Mittleenthal, Lisa Nagy, Garrett Odell, Jarmila Kukalova-Peck, Louise Roth, Günter Wagner, and William Wimsatt. To the workshop proceedings and participants we owe much of the development of our thinking on the topics discussed in this essay and several of the examples discussed, and we are forever grateful to the participants for sharing their thoughts and collegiality both during the workshop and after. We express our appreciation to the Friday Harbor Laboratories, its staff, and director for a wonderful environment for a meeting. We are also especially grateful to Dr. Evelyn Fox Keller for encouraging us in these directions, for the idea of a workshop on modularity, and for providing the bulk of the funding for that workshop out of her own pocket.

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Modularity In Development And Evolution

Lei Huang



Modularity In Development And Evolution:

Modularity in Development and Evolution Gerhard Schlosser, Gunter P. Wagner, 2004-07 Modularity in Development and Evolution offers the first sustained exploration of modules from developmental and evolutionary perspectives Contributors discuss what modularity is how it can be identified and modeled how it originated and evolved and its biological significance Covering modules at levels ranging from genes to colonies the book focuses on their roles not just in structures but also in processes such as gene regulation Among many exciting findings the contributors demonstrate how modules can highlight key constraints on evolutionary processes A timely synthesis of a crucial topic Modularity in Development and Evolution shows the invaluable insights modules can give into both developmental complexities and their evolutionary origins

Modularity Werner Callebaut, Diego Rasskin-Gutman, 2005 Modularity the attempt to understand systems as integrations of partially independent and interacting units is today a dominant theme in the life sciences cognitive science and computer science The concept goes back at least implicitly to the Scientific or Copernican Revolution and can be found behind later theories of phrenology physiology and genetics moreover art engineering and mathematics rely on modular design principles This collection broadens the scientific discussion of modularity by bringing together experts from a variety of disciplines including artificial life cognitive science economics evolutionary computation developmental and evolutionary biology linguistics mathematics morphology paleontology physics theoretical chemistry philosophy and the arts The contributors debate and compare the uses of modularity discussing the different disciplinary contexts of modular thinking in general including hierarchical organization near decomposability quasi independence and recursion or of more specialized concepts including character complex gene family encapsulation and mosaic evolution what modules are why and how they develop and evolve and the implication for the research agenda in the disciplines involved and how to bring about useful cross disciplinary knowledge transfer on the topic The book includes a foreword by the late Herbert A Simon addressing the role of near decomposability in understanding complex systems Contributors Lee Altenberg Lauren W Ance Meyers Carl Anderson Robert B Brandon Angela D Buscalioni Raffaele Calabretta Werner Callebaut Anne De Joan Rafael Delgado Buscalioni Gunther J Eble Walter Fontana Fernand Gobet Alicia de la Iglesia Slavik V Jablan Luigi Marengo Daniel W McShea Jason Mezey D Kimbrough Oller Domenico Parisi Corrado Pasquali Diego Rasskin Gutman Gerhard Schlosser Herbert A Simon Roger D K Thomas Marco Valente Boris M Velichkovsky Gunter P Wagner Rasmus G Winter Vienna Series in Theoretical Biology

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modules can highlight key constraints on evolutionary processes A timely synthesis of a crucial topic Modularity in Development and Evolution shows the invaluable insights modules can give into both developmental complexities and their evolutionary origins *The Epistemology of Development, Evolution, and Genetics* Richard Burian,2005 These essays examine the developments in three fundamental biological disciplines embryology evolutionary biology and genetics These disciplines were in conflict for much of the 20th century and the essays in this collection examine key methodological problems within these disciplines and the difficulties faced in overcoming the conflicts between them Burian skillfully weaves together historical appreciation of the settings within which scientists work substantial knowledge of the biological problems at stake and the methodological and philosophical issues faced in integrating biological knowledge drawn from disparate sources *Encyclopedia of Evolutionary Biology* ,2016-04-14 Encyclopedia of Evolutionary Biology Four Volume Set is the definitive go to reference in the field of evolutionary biology It provides a fully comprehensive review of the field in an easy to search structure Under the collective leadership of fifteen distinguished section editors it is comprised of articles written by leading experts in the field providing a full review of the current status of each topic The articles are up to date and fully illustrated with in text references that allow readers to easily access primary literature While all entries are authoritative and valuable to those with advanced understanding of evolutionary biology they are also intended to be accessible to both advanced undergraduate and graduate students Broad topics include the history of evolutionary biology population genetics quantitative genetics speciation life history evolution evolution of sex and mating systems evolutionary biogeography evolutionary developmental biology molecular and genome evolution coevolution phylogenetic methods microbial evolution diversification of plants and fungi diversification of animals and applied evolution Presents fully comprehensive content allowing easy access to fundamental information and links to primary research Contains concise articles by leading experts in the field that ensures current coverage of each topic Provides ancillary learning tools like tables illustrations and multimedia features to assist with the comprehension process **Toward a Theory of the Evolution of Modularity Using**

Sequential-subtask Environments and Development Jessica Lowell,2017 This dissertation builds toward a theory of the evolution of modularity by investigating specific techniques for promoting the evolution of different kinds of modularity and using them to discuss a larger framework It examines environmental and biological process inspired methods for promoting the evolution of modularity both within different levels of abstraction and in terms of hierarchical organization and makes a case for the specific mechanisms involved Sequential subtask environments are found to promote the evolution of both single level and hierarchical modularity Adding development to the evolutionary process also promotes the evolution of hierarchical modularity When sequential subtask environments and development are combined the results are strongly hierarchically modular Development appears to prevent single level modularity from dropping over the course of evolution Using number of species evolved as a proxy for the complexity of the evolutionary search space fitness landscape suggests that in sequential

subtask environments the search space is more complex compared to that in single task or parallel task ones and in evolutionary developmental systems compared to evolutionary ones A taxonomy of different methods for promoting modularity is described and the results of my experiments are placed within that taxonomy *The Routledge Companion to Philosophy of Psychology* Sarah Robins, John Symons, Paco Calvo, 2019-10-08 The Routledge Companion to Philosophy of Psychology Second Edition is an invaluable guide and major reference source to the key topics problems concepts and debates in philosophy of psychology and is the first companion of its kind A team of renowned international contributors provide forty eight chapters organized into six clear parts Historical background to philosophy of psychology Psychological explanation Cognition and representation The biological basis of psychology Perceptual experience Personhood The Companion covers key topics such as the origins of experimental psychology folk psychology behaviorism and functionalism philosophy psychology and neuroscience the language of thought modularity nativism and representational theories of mind consciousness and the senses dreams emotion and temporality personal identity and the philosophy of psychopathology For the second edition six new chapters have been added to address the following important topics belief and representation in nonhuman animals prediction error minimization contemporary neuroscience plant neurobiology epistemic judgment and group cognition Essential reading for all students of philosophy of mind science and psychology The Routledge Companion to Philosophy of Psychology will also be of interest to anyone studying psychology and its related disciplines [Annual Review of Ecology, Evolution, and Systematics](#) ,2008 **From Plant Taxonomy to Evolutionary Biology** Peter K. Endress, 2005

Science John Michels (Journalist), 2004 A weekly record of scientific progress [Tinkering](#) Novartis Foundation, 2007-07-23 Much recent research in evolutionary developmental biology has focused on the origin of new body plans However most evolutionary change at the population and species level consists of tinkering small scale alterations in developmental pathways within a single body plan Such microevolutionary events have been well studied on a population genetic level and from the perspective of adaptive phenotypic evolution but their developmental mechanisms remain poorly studied This book explores both theoretical and practical issues of tinkering It features a wide range of perspectives to address several fundamental questions How does tinkering occur developmentally and how is it manifested phenotypically Are the developmental mechanisms by which tinkering occur different from those that underlie larger evolutionary changes What are the developmental constraints on tinkering And how do we test hypotheses about microevolutionary shifts in development from the fossil record With contributions from experts in a range of fields this fascinating book will make exciting reading for anyone studying evolution developmental biology or genetics [Keywords and Concepts in Evolutionary Developmental Biology](#) Brian K. Hall, Wendy M. Olson, Wendy Olson, 2003-05-30 Covering more than 50 central terms concepts the entries in this reference offer an overview of all that is embraced by the subdiscipline of evolutionary developmental biology providing core insights ideas that show how embryonic development relates to life history evolution

adaptation **Michigan Law Review** ,2006-03 **Handbook of Evolution** Franz M. Wuketits, Christoph Antweiler, 2004 This two volume handbook is unique in spanning the entire field of evolution from the origins of life up to the formation of social structures and science and technology The author team of world renowned experts considers the subject from a variety of disciplines with continuous cross referencing so as to retain a logical internal structure The uniformly structured contributions discuss not merely the general knowledge behind the evolution of life but also the corresponding development of language society economies morality and politics The result is an overview of the history and methods used in the study of evolution including controversial theories and discussions A must for researchers in the natural sciences sociology and philosophy as well as for those interested in an interdisciplinary view of the status of evolution today **On the Germ-soma Distinction in Evolutionary Biology** Grant Joo Yamashita, 2006 **The Innate Mind** Peter Carruthers, Stephen Laurence, Stephen P. Stich, 2005 This is the third volume of a three volume set on The Innate Mind The extent to which cognitive structures processes and contents are innate is one of the central questions concerning the nature of the mind with important implications for debates throughout the human sciences By bringing together the top nativist scholars in philosophy psychology and allied disciplines these volumes provide a comprehensive assessment of nativist thought and a definitive reference point for future nativist inquiry The Innate Mind Volume 3 Foundations and the Future concerns a variety of foundational issues as well as questions about the direction of future nativist research It addresses such questions as What is innateness Is it a confused notion What is at stake in debates between nativists and empiricists What is the relationship between genes and innateness How do innate structures and learned information interact to produce adult forms of cognition e g about number and how does such learning take place What innate abilities underlie the creative aspect of language use and of creative cognition generally What are the innate foundations of human motivation and of human moral cognition In the course of their discussions many of the contributors pose the question whether explicitly or implicitly Where next for nativist research Together these three volumes provide the most intensive and richly cross disciplinary investigation of nativism ever undertaken They point the way toward a synthesis of nativist work that promises to provide a powerful picture of our minds and their place in the natural order **The Year in Evolutionary Biology** ,2010 Proceedings ,2007 **Compositional Evolution** Richard A. Watson, 2006 In *Compositional Evolution* Richard Watson uses the tools of computer science and computational biology to show that certain mechanisms of genetic variation such as sex gene transfer and symbiosis allowing the combination of preadapted genetic material enable an evolutionary process compositional evolution that is algorithmically distinct from the Darwinian gradualist framework Jacket **The American Naturalist** ,2006

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