

1 The Ubiquity of Modularity

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In our world, modular systems, both natural and artificial (in Herbert Simon's sense¹), abound. The majority of the contributions to this volume deal with modularity as uncovered and specified in a number of biological disciplines. Part II deals with the challenge modularity poses for evolutionary biology, developmental biology, and the emerging interfield between evolution and development usually referred to as evolutionary developmental biology or *evo-devo*.² Part III considers the implications of modularity for macroevolution, morphology, and paleobiology. While the focus in part II is on process ("The Making of a Modular World"), the emphasis in part III is more structural ("Working Toward a Grammar of Forms"). Part III also includes chapters on modularity in art and at the boundary between art and science. The fourth and last part of the book deals with mind and culture. The vexed question of the modularity of the human mind is framed in the context of advancements in artificial intelligence, neuroscience, and the cognitive sciences in general, with a particular emphasis on connectionism. It is also argued here that although "modularity" is not normally part of the terminology of social scientists (but see Baldwin and Clark, 1997; Hurley, 1999), the realm of economic interactions provides almost ideal field and laboratory settings to study modularity.

Because the editors of this volume view minds and cultures as well as their exosomatic products (technologies) as naturally evolved and naturally developing systems, we insist on subsuming them all under "natural complex systems," as the subtitle of the book indicates. (The view that modularity is a prerequisite for adaptive technological evolution as well as for biological evolution has been popularized by the influential work of the economic historian Paul David and others on the robustness of the QWERTY system.³) The final chapter in the book is concerned with the "natural logic" of communicative possibilities, extending the concept of morphospace that was central to part III to the (human and animal) psychological and cultural realms.

This introductory chapter is concerned primarily with providing some conceptual foundations for the enterprise that follows. I will first suggest that there is an intimate connection between the ubiquity of modular organization in the world and the circumstance that Western science has *historically* been so successful at "the knowledge game" (Hull, 1988)—which is not to deny that science may also be successful at understanding, say, nonmodular deterministic systems or chaotic systems (see Agre, 2003 on the evolutionary significance and generalizability of Simon's parable of the two watchmakers). Moreover, with Simon, I would argue that we

already do possess more—and better—than “transcendental” arguments for the ubiquity of evolved modules, and thus can at least begin to genuinely *explain* the ubiquity of modularity.

Next I will look at a number of contexts in which scientists deem it necessary or useful to invoke modularity, try to disentangle various meanings and uses of the word (e.g., as *explanans* or *explanandum*), and attempt to provide as general a definition of modularity as possible, with a view to the wide range of applications considered in this book. I then will look in some detail at the biological uses of modularity, in particular in the contexts of development and evolution. I will round off this chapter by discussing some aspects of the issue of the modularity of the mind/brain.

“Fortune Smiled upon Kepler and Newton”

The success of modern science depends on plausible simplification. The number of actual or conceivable interactions among the parts of a system greatly exceeds the number of interactions that must actually be taken into account to yield system descriptions that are good enough for most theoretical or practical purposes. This happy condition was critical for the articulation of classical mechanics—the paradigmatic science of *simplicity*. Imagine a system that grows by multiplying its parts (or by the agglomeration of smaller systems; see Foreword in this volume). The number of potential interactions between the system’s parts will increase much more quickly than its cardinality (number of parts). To illustrate this point, Simon (1977b) described an episode that from the perspective of the history of science has been of dramatic importance in that it consolidated the Scientific Revolution substantially. Because this example provides the starting point for my argument concerning the ubiquity of modularity, I think it is worthwhile to discuss it in some detail.

Consider our solar system as it was known in Kepler’s and Newton’s day. It consisted of a sun, six planets (including Earth), and about ten visible satellites belonging to three of the planets. (Comets are left out of the picture.) If one considers only pairs of heavenly bodies, there are already $17 \times 16 = 272$ potential interactions between the elements of the system (half as many if one assumes that $I(a,b)$ and $I(b,a)$ represent identical interactions), resulting in a rather complex description of the system. Note that there is no *a priori* reason to assume that the system’s behavior is determined only by pairs of bodies, although Newtonian physics did make this assumption. It turns out that in practice, one does not have to take into account most of these potential interactions:

Kepler and Newton did no such thing. Kepler detected three observational regularities: the orbits of the planets about the sun are ellipses with the sun at the focus; equal areas are swept out in a given planetary orbit in equal times; and the periodic times of the planets vary with the $3/2$ power of their distances from the sun. Newton showed that these phenomena, together with the analogous ones for the satellites, could be deduced from his Laws of motion, taken in combination with the gravitational law, gravitational force varying inversely with the square of the distance between a pair of bodies. But the observed regularities, and the derivation as well, depended upon the assumption that each particular orbit under consideration was determined by the interaction between the sun and a single central body (a planet or satellite). In each case, interactions with all other components of the system were ignored, and yet an excellent fit was obtained between the theoretical derivations and the observations. (Simon, 1977b, pp. 508–509)

Why were such elementary calculations sufficient?⁴ The explanation, Simon argued, is to be sought in the circumstance that our solar system, in comparison with the kinds of solar systems one would expect on the basis of purely statistical considerations, turns out to be a very special case indeed. “If the deck of cards that Nature dealt to Kepler and Newton was not stacked, it was at least a very lucky deal.” Why was this so? Simon continues:

First there was a single body, the sun, that was larger by three orders of magnitude than any other body in the system. Second, there were six bodies, the planets, that were several orders of magnitude larger than their satellites. Third, the distances of the planets from each other were of the same order of magnitude as their distances from the sun, while the distances of the satellites from their planets were orders of magnitude smaller than their distances from the sun. *None of these distributional facts follows from the laws of mechanics but had they not been true of the solar system, Kepler’s regularities and Newton’s derivations would not have described that system.* Although Newton’s Laws are generally valid (up to the classical, non-relativistic approximation) for systems of masses, the relatively simple calculations used to test those laws would not have sufficed had the system been more “general.” Because of these relative sizes and distances, each planet orbited around the sun almost exactly as if it had been attracted by the sun alone, and each satellite around its planet in a similar way. (Simon, 1977b, p. 509; italics added)

These simplifications depended not only on the distribution of masses and distances; they were amplified by the *forms of the laws* themselves (Simon, 1997b, p. 509). For these several reasons, our solar system is simpler—and hence can be treated as such⁵—than one would expect on the basis of 272 pairwise interactions. Most interesting is the fact that this “fortune” also extends, albeit often less spectacularly, to the natural complex systems scientists are now beginning to understand (see, e.g., Székely, 2001 for an application of “Simon’s theorems” to the complexity of the brain). The possibility of scientific understanding crucially depends, then, on the *near decomposability* (Simon) of modular systems, which allows the subdivision of the

explanatory task into manageable chunks. Generally speaking, a system may be characterized as modular to the extent that each of its components operates primarily according to its own, intrinsically determined principles. Modules within a system or process are tightly integrated but relatively independent or “dissociable” (Needham, 1933) from other modules (e.g., Simon, 1969, 1973, 1977b, 1995; and Foreword in this volume; Raff, 1996; Wagner, 1996). Because the strength or weakness of interactions is a matter of degree, modularity should itself be seen as a gradual property (see Wagner and Altenberg, 1996 and chapters 2 and 9 in this volume).

Explaining the Ubiquity of Modularity

Let us suppose that most of the natural complex systems that science encounters do display the nearly decomposable organization—characterized by “meager” (i.e., thinly populated) interaction patterns that Simon and other systems theorists have described.⁶ As Simon has emphasized, philosophers and other skeptics could easily object that this “fact” tells us little or nothing about the structure of reality but could be due, entirely or in part, to the perceptual and/or analytical biases of limited human epistemic subjects (see my discussion of Brandon below, as well as chapter 13 in this volume). On this quite influential view, the universe could well be ultra-complex, but will remain barred to us, presumably forever.

My reply to this is threefold. First, there are general reasons to resist “global skepticism,” which as far as science is concerned has been shown to be a doomed heuristic (see Shapere, 1984). Second, pace evolutionary epistemologists and evolutionary psychologists who claim that our evolutionary heritage has inescapably “bleak implications” for human rationality (but see Samuels et al., 1999), the progress of science hitherto suggests no principal reasons whatsoever, and certainly no a priori reasons, to doubt that our science, through the improvement of its observational, experimental, and computational techniques, will be able to transcend any such limitations (see, most forcefully, Levinson, 1982; see also Callebaut and Stotz, 1998). Although, say, evidence from the anthropology of science suggests that work in taxonomy to date remains tributary to folk-biological categories (Atran, 1998) and that “psychological essentialism” (Barrett, 2001) may be the result of a history of natural selection on human representation and inference systems,⁷ the very same work also indicates that scientists *are* able to reflexively overcome their remnant anthropocentrism.

Third, in the vein of Simon’s a posteriori arguments concerning classical mechanics, it is very possible to look for, say, the *biological* reasons why “the bodies of higher

organisms are so obviously built in a modular way such that apparently natural units are often easy to recognize” (Wagner, 1996, p. 36). As Wagner puts it in his discussion of homologues, “Homologues, if they are natural kinds, do not exist in order to serve the needs of comparative anatomists” (1996, p. 36; see also Wagner and Laubichler, 2000 on the role of the organism in character identification).⁸

A perhaps more serious objection concerns the logic of influential arguments for the ubiquity of (evolutionary-developmental) modularity by Lewontin and Bonner. Lewontin (1974) stressed the “quasi independence” of characters, by which he meant that there are at least some developmental trajectories that allow one character to be changed without affecting others. Bonner (1988) considered “gene nets,” groupings of networks of gene actions and their products into discrete units during the course of development. As Brandon (chapter 3 in this volume) makes clear, Bonner’s and Lewontin’s arguments are “transcendental” in that they claim that modularity is *necessary* for the very existence of the phenomena of adaptation: “Adaptive evolution, which produces the phenomena of adaptation, requires quasi independence/gene nets. The phenomenon of adaptation is real. Therefore, quasi independence/gene nets exist.” The problem with transcendental arguments, Brandon states, is that although they are perfectly valid from a logical point of view, they are not explanatory (see Brandon, 1999, p. 178, n. 11). Also, and perhaps more important, they may unwittingly reflect limitations on our understanding of the world rather than a limitation on how the world works.

Brandon’s diagnosis seems to me to be convincing as far as the cases at hand are concerned. But is this grounds to worry about the feasibility of the general enterprise of trying to explain the ubiquity of modularity—and, conversely, its limitations—as, say, a variational principle? Brandon himself points the way when he writes that belief in the existence of evolutionary modules may be inferred “indirectly” from phylogenetic data or based on the “direct” observation of modules.

This is in fact what current practice tries to do. For instance, Jablonka (2001), in her comparison of the genetic inheritance system (GIS) with epigenetic (EIS), behavioral (BIS), and symbolic (SIS) inheritance systems, identifies both modular and nonmodular (“holistic”) types of information and modes of transmission of information. Only the GIS, methylation (one of the several EISs she describes), and imitation and teaching (two of the several BISs) concern purely modular information that is also transmitted in a purely modular way; symbolic systems, which are transmitted by social learning, are transmitted both modularly and holistically.

Or, to take another example, the question whether genetic modularity is necessary for evolvability (i.e., the ability to respond to a selective challenge by producing the right kind of variation; see, e.g., Gerhart and Kirschner, 1998; Raff and Raff,

2000; cf. Wagner and Laubichler, 2004, pp. 100–101) can be tackled by putting it in the context of other conceivable principles of evolvability. Hansen (2003) lists quite a few alternative candidates: co-optation, cryptic variation, dissociability, duplication and divergence, “the edge of chaos,” “evolutionary cranes” (Dennett, 1995), “extradimensional bypass” (Conrad, 1990), recombination, redundancy, robustness, symmetry, and—if this can be viewed as different from modularity itself—the emergence of new hierarchical levels of organization.

Reminding us of François Jacob’s metaphor of evolution as tinkering, Hansen cautions that while genetic modularity “may indeed be a simple, logical and efficient way of achieving evolvability,” it does not follow that it *is* the biological basis of evolvability. (But see chapter 9 in this volume, where Rasskin-Gutman postulates that the space of modular design is the only available pool for the evolutionary arrow to proceed.) Nor is it to be excluded that genetic evolvability is achieved “in ways that appear complex and illogical to our minds” (Hansen, 2003, p. 85). In the scenario Hansen considers, the most evolvable genetic architectures are typically those with an intermediate level of integration among characters, and in particular those where pleiotropic effects are variable and able to compensate for each other’s constraints. Several of the chapters in this volume probe other such scenarios. This and related work seem to indicate that the question “Why does complexity in our universe, at virtually all levels, generally take this hierarchical, nearly decomposable form?” (Simon, foreword to this volume) is clearly amenable to theoretical and empirical investigation that can lead to genuinely explanatory answers (see chapter 11 in this volume). At least *some* transcendental arguments can be “naturalized”! Since chapter 2 deals entirely with the origin of modules, this important but vexed issue will not be further pursued here.

Dimensions and Kinds of Modularity

At this juncture I will introduce a number of conceptual distinctions in order to prepare the reader for the somewhat bewildering panorama of modularities awaiting her. Modules are invoked in many different contexts with different purposes, some of which have little in common with our preoccupations in the present volume. Yet it seems fair to say that there is a sense that runs through *any* ascription of modularity, from the art motifs discussed in chapters 12 and 13 of this volume to chapter 17’s autonomous and anonymous economic agents who take decisions independently from one another and interact only through the price system. It is that “of a unit that is a component part of a larger system and yet possessed of its own structural and/or functional identity” (Moss, 2001, p. 91). In addition to the criteria of

tight internal integration and relative independence from other modules introduced above, this characterization suggests two further criteria: that modules must *persist* as identifiable units for long enough time spans (or, in the case of evolutionary modules, generations), and that they must be more or less identical, *repetitive*, and reusable “building blocks” of larger wholes and/or different systems (e.g., Müller and Wagner, 1996; Müller and Newman, 2003).

Both of the latter criteria indicate that modules may be subject to a certain amount of change within them (Raff, 1996, p. 322; Gilbert and Bolker, 2001, p. 10). For instance, the economic agents of classical and neoclassical economic theory discussed in chapter 17 of this volume must live long enough to participate in market transactions such as working for a salary, buying or selling goods, and the like; and there must be large enough populations of these agents for markets to be able to function properly. Or, to take another example, developmental modules can be deployed repeatedly in the same organism, as in the case of the left and right forelimb buds. The two forelimbs are two *different developmental modules* of the organism, but they are also parts of the *same evolutionary module* (chapter 2 in this volume).

Still at this most general level, “ontologically” speaking, modularity comes in two varieties: “It may be a primary property of the way organisms are built, for instance due to organizational principles of self-maintaining systems” (Fontana and Buss, 1994), or it may be an “evolved property” (Wagner, 1996, p. 38). If modular organization is the product of evolution by natural selection—the only evolutionary force capable of explaining adaptation on the standard, neo-Darwinian view (e.g., Ridley, 1993, part 3)—it can result either from *parcellation* (i.e., the differential elimination of pleiotropic effects among characters belonging to different character complexes) or from the differential *integration* of independent characters serving a common functional role. The relative frequency of either is an empirical question (Wagner, 1996, pp. 38–39). I will return to the issue of evolutionary modules below.

Structure, Process, and Function

Still at this level of greatest generality, it seems useful and even imperative to distinguish modularity of *structure* from modularity of *process*. Whereas at least the identification of structural or architectural modules is often a straightforward matter (Bolker, 2000), many biologists have been reluctant to talk about process modules because they would seem to be much more ephemeral. In biology at least, the issue is further complicated by the circumstance that modularity and *homology* have a common (recent) history (Wagner, 1995, 1996; Moss, 2001). As late as 1971, De Beer “drew a clear line between structure, which he viewed as the only appropriate thing

to be homologized, and function: ‘An organ is homologous with another because of what it is, not because of what it does’” (Gilbert and Bolker, 2001, p. 1).

Recent progress in developmental genetics has led to remarkable insights into the molecular mechanisms of morphogenesis, but has at the same time blurred the clear distinction between structure and function that De Beer was relying on. Gilbert and Bolker (2001, p. 10) are confident that “[i]dentifying the ways in which homologous processes are regulated, replicated and changed over time will enable us to better understand how changes in development generate changes in morphology and, ultimately, the evolution of new groups of animals.” More generally, process modularity is required to make sense of modular *functions*, which are behaviors, not structures.⁹ (Recall Moss’s definition of a module as “a unit that is a component part of a larger system and yet possessed of its own structural and/or functional identity,” introduced above.)

Following Bechtel and Richardson, whose work on decomposition and localization as research strategies in the biological and cognitive sciences is in many ways an elaboration and refinement of Simon’s view on near decomposability, I want to frame this issue in the context of sound—which for me means *mechanistic*—explanation (see Callebaut, 1989, 1995):

Simple localization differentiates tasks performed by a system, localizing each in a structural or functional component. Complex localization requires a decomposition of systemic tasks into subtasks, localizing each of these in a distinct component. Showing how systemic functions are, or at least could be, a consequence of these subtasks is an important element in a fully mechanistic explanation. Confirming that the components realize those functions is also critical. Both are necessary for a sound mechanistic explanation. (Bechtel and Richardson, 1993, p. 125)

It is important to note that structures often do not map neatly one to one onto functions (and vice versa), making functions indispensable. As Bechtel and Richardson show, the route to complex localization frequently begins with direct localization, which then develops into a more complex localization in which functional decomposition of tasks becomes more central (see Star, 1989). This is common in psychology, where research often begins by dividing psychological activities into broad performance categories such as perception, memory, language, reasoning, and emotion. Bechtel and Richardson note that “Noam Chomsky has provided one of the clearest expressions of this approach in his own ‘organology’, strikingly reminiscent in tone of phrenology” (p. 126). Fodor has generalized Chomsky’s organology, or modularity, beyond the domain of language to modular cognitive systems, which he claims are “domain specific, innately specified, hardwired, autonomous, and not assembled” (Fodor, 1983, p. 37). I will return to the issue of cognitive

modules later on. Again with a view to mechanistic explanatory concerns, Von Dassow and Munro (1999, pp. 307–308) write:

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 development or as units of evolutionary change.

Top-Down and Bottom-Up Research Strategies

Quite often, modules have been or are posited “top-down,” beginning the investigation with the phenomenal properties of a system, and then attempting to explain its working on the basis of one or several modules. Cognitive science abounds with examples (Bechtel and Richardson, 1993). Such modules, like the “Darwinian” modules postulated in evolutionary psychology and related “massive modularity” accounts (see below), have not been empirically observed but, in straightforward Popperian fashion, speculatively brought forth as *explanans* (Moss, 2001; see also chapter 9 in this volume). Modules of this sort are quite often associated with a preformationist stance, as in Chomsky’s and Fodor’s view or, more recently, in evolutionary psychology, where

The cognitive capacity/phenotype (whether still of adaptive value or not) is . . . construed to be the expression of a developmentally invariant, preformationistically transmitted module that has been passed along from generation to generation ever since [the Pleistocene]. (Moss, 2001, p. 92)

Yet, as Moss points out, “the concept of module itself does not specify its place along a preformationism–epigenesis axis” (2001, p. 92). Clear-cut examples of the converse, “bottom-up” research strategy may be found in, say, computer programming and neurocomputing (e.g., Barbuti et al., 1993; Husken et al., 2002) or in the ab initio calculations of artificial life (e.g., Adami 2002; see also Fontana and Buss, 1994). As Moss (2001, p. 92) notes, “the ‘genetic revolution’ of the twentieth century did not result in a search for any form of subcellular modules, nor any expectation of finding such. Rather, the recognition of modularity came as a surprise.” At least in subcellular biology, modularity has arisen as an *explanandum* in the first place, but by now, new and promising module-centered explanatory approaches have begun to emerge which usefully complement many developmental accounts (see below).¹⁰ The bottom-up versus top-down distinction should not be pushed too far, however. In the end, modularity becomes “all-around” as the modules are recognized, characterized, and used empirically. Once a module has been established, its

constituent parts become irrelevant, so to speak (see Simon's "pragmatic holism" as discussed in chapter 15 of this volume). What matters most from now on is the interaction among modules.

Biological Modules

For the purposes of my discussion of biological modularity, it will be convenient to distinguish three aspects: development, morphology, and evolution.

Developmental Modularity

Although many of the structures and processes with which developmental biologists have been traditionally concerned are readily referred to as "developmental modules," it is not always clear what this is supposed to mean or imply. Von Dassow and Munro (1999, p. 308) warn that at present we have only the "rudiments of a developmental modularity concept," which comprise many intuitive notions about modularity (Raff, 1996, esp. chap. 10), including morphogenetic fields (Gilbert et al., 1996), gene networks (Bonner, 1988), and the several notions of homologues (Hall, 1992). One way to define developmental modules operationally is to state that any subsystem manifesting some quasi-autonomous behavior qualifies (Von Dassow and Munro, 1999, p. 313).

According to the current "interactionist consensus" that emerged from nature/nurture debates (Kitcher, 2001; Oyama et al., 2001), developmental modules are viewed as "phenotypic expressions of genes in an environment" (Sperber, 2002). But at least since the hardening of the Modern Synthesis, in practice the environment typically has been left out of the picture (see Robert et al., 2001).¹¹ "In genetic experiments, variability that was associated with flexibility and condition-sensitive development came to be regarded as noise, a factor to be controlled and not studied for its own sake" (West-Eberhard, 1998, p. 8417). Worse, common practice also suppresses the important roles that *epigenetic* factors play in development as well as in evolution, although "epigenesis is a primary factor directing morphological evolution, even in evolved developmental systems" (Newman and Müller, 2000, p. 312; see also Griesemer, 2002; Müller and Olson, 2003). Thus the tendency to black-box development that had been inaugurated by Darwin (Amundson, 1994) is continued.¹² "Molecular developmental systems" is one among several recent attempts to counteract this: "A necessary molecular concomitant of organismal complexity appears to be that of great developmental versatility in the resources available for constructing cell-to-cell and cell-to-matrix linkages" (Moss, 2001, p. 93).

As Sterelny (2001, p. 341) emphasizes, an important feature of developmental modules is their *reusability*. Müller and Wagner describe the “machinery of development” as follows:

The more we learn about molecular mechanisms of development in widely different organisms, the higher the number of conserved mechanisms that become known. Some of them do indicate homology of morphologically divergent characters. . . . Still others illustrate that highly conserved molecular mechanisms may be used in radically different developmental contexts, indicating that the machinery of development consists of modular units that become recombined during evolution. (Müller and Wagner, 1996, p. 11)

At the very least, such insights suggest that biological reality is much too complex to be captured by a linear mapping of genes onto developmental schedules, and of developmental schedules onto phenotypes (Minelli, 1998). The extent and functional basis of developmental modularity will need to be investigated in much greater detail, however (see Griffiths and Gray, 2001, p. 215).

Morphological Modularity

At the *morphological* or architectural level, the structure and function of specific parts or elements of organisms like the mammalian forelimb or the modular structures of animal skeletons are characterized (see, e.g., Riedl, 1978). The contributions of modularity in art in part III and some of the chapters on neurocognitive modularity in part IV also concentrate on architectural aspects. At this level, a part is to be viewed as a module in what might be called the “operation” of an organism, for example, in its physiology or behavior, rather than its development (chapter 8 in this volume). Alternatively, morphological modules may be seen as preserving the functional integrity of the part but not its purposive function (chapter 9 in this volume).

As Thomas’s discussion (chapter 11 in this volume) of animal skeletons as nearly decomposable systems shows, individual elements may have “a relatively high degree of local, short-run integrity of structure and function, while being interdependent at the level of operation of the organism as a whole.” The structural elements defined by the parameters of Thomas’s *skeleton space* may be skeletons in themselves, parts of skeletons, or parts of tightly integrated skeletal complexes with specific functions. At this level, biologists are increasingly interested in the way in which organisms and their parts can be viewed as an articulation of more or less autonomous mechanisms. See, for example, chapter 8 in this volume on the “remodularization” of organisms in the evolutionary transition from single-cell to multicellular organisms, or chapter 9 in this volume, where modularity is characterized

as integration on four different morphological levels: proportions, orientations, connections, and articulations.

Eble (chapter 10 in this volume) notes that “the parts and characters routinely identified by the morphologist reflect hypotheses of modularity based on observational or quantitative criteria, without reference to the generative mechanisms or the theoretical contexts to which modules relate.” However, a notion of developmental modularity in terms of mechanisms of genetic and epigenetic specification of units of phenotypic evolution is now being advanced (see below). Since morphological patterns of organization emerge in ontogeny, “morphological modularity might thus be seen as an aspect of developmental modularity” (chapter 10 in this volume). See also chapter 9 in this volume on morphological modularity as a consequence of binary division in multicellular organisms.

Evolutionary Modularity

As elaborated in various ways in part II of this volume, the concept of modularity provides a powerful nexus between developmental and evolutionary questions (see esp. chapter 4 in this volume). Perhaps most important, there turns out to be an intimate connection between continued *evolutionary plasticity* in a lineage and developmental modularity (Wagner, 1995; Müller and Wagner, 1996; Raff, 1996; Wagner and Altenberg, 1996; Brandon, 1999 and chapter 3 in this volume; Bolker, 2000; see also Dawkins, 1996, on “kaleidoscope embryology”). I have already mentioned Lewontin’s argument for the necessity of “quasi independence” of characters and Bonner’s view of “gene nets”—adaptive change would be impossible if development were holistic. Wagner and Altenberg (1996) have translated this point in the language of genotype–phenotype mappings. On this view, an evolutionary module is “a set of phenotypic features that are highly integrated by phenotypic effects of the underlying genes and are relatively isolated from other such sets by a paucity of pleiotropic effects” (see chapter 2 in this volume, esp. figure 2.1).

Thus the *genetic representation* (see chapter 17 in this volume) is modular. In the same vein, a *module of selection* may be defined as “a set of genes, their products and interactions (their developmental pathways), the resulting character complex and that complex’s functional effect” (Brandon, 1999, p. 177). This, Brandon suggests, is what evolution by natural selection “picks out, selects among, and transforms,” implying at long last a solution to the units and levels of selection riddle: “These modules are the units of evolution by natural selection” (1999, p. 177; see also chapter 7 in this volume).

Moss (2001, pp. 87–88) usefully distinguishes between “Genes-P” and “Genes-D.” A Gene-P is defined in terms of its functional relationship to a phenotype, “black-

boxing,” as it were, requirements in regard to specific molecular sequence, and with respect to the biology involved in producing the phenotype (e.g., a “gene for blue eyes”). A gene-D, in contrast, is “mechanistically” defined by its molecular sequence. It is a developmental resource in the sense of Developmental Systems Theory (Oyama et al., 2001) and, as such, “indeterminate” with respect to phenotype. See also Wheeler and Clark (1999) on the analogy of genes in the production of biological form and the role of neural states in the production of behavior, and in particular their discussion of “causal spread.” Using this distinction, Moss describes how modularity and homology have come together as complementary themes arising out of research in subcellular biochemistry and molecular biology:

Modularity, at the level of individual genes (Gene-D), which is the rule not the exception for the eukaryotic cell and all metacellular organisms, provides for developmentally contingent flexibility in the expression and realization of “gene-products” from out of the resource base which any Gene-D represents. N-CAM is just such a modularized Gene-D resource, but it is also just one member of a “superfamily” of modularized genetic resources whose kinship is defined by the possession of homologous modules. . . . Much of the evolutionary novelty associated with increasing organismic complexity, it turns out, has been achieved through the reshuffling and mixing and matching of modular exon units to form families of homologous genetic (Gene-D) resources. This has been particularly pronounced with respect to those molecules associated with developmentally and functionally contingent associations between cells and other cells, and cells and extracellular matrices. (Moss, 2001, p. 93; more details in Moss, 2003)

In the modeling scenarios of Schank and Wimsatt, unless development is modular, phenotypes will become *generatively entrenched*, for a change in a developmental sequence is likely to ramify, having many effects on the developed phenotype, some of which would be deleterious (Schank and Wimsatt, 1988, 2001; Wimsatt and Schank, 1988).

Neural and Cognitive Modules

With one exception, all of the chapters in part IV directly or indirectly address the issue of neurocognitive modularity, or at least the question of how the brain and the mind are to be meaningfully interrelated. (The exception is chapter 17, which elaborates Simon’s view with respect to the economic realm, showing neatly how classical economic theory can be seen to display modularity in its purest form, and offering a new take on problems we have encountered, such as the problem of genetic representation, along the way.) Chapter 16, on the attractiveness and pitfalls of cognitive modularity in general, and the more specialized treatments of

evolutionary connectionism and mind/brain modularity in chapter 14, of modularity in “classical” information-processing models in chapter 15, and of the modular elements that are an integral part of Oller’s “natural logic of communicative capabilities” in chapter 18 are all remarkably self-contained, and as such would not require much by way of conceptual preparation here. However, since they are also critical of the computational approach that continues to dominate the cognitive sciences to this day, it should be worthwhile to critically survey some of the developments and views they are responding to—in particular, evolutionary psychology.

Neural Modularity

The modular conception of the human brain goes back at least to the efforts to explain the uniqueness of our species by such pioneers as Pierre-Paul Broca (1824–1880), Carl Wernicke (1848–1904), and—yes—Sir Russell Brain (1895–1966), who sought to discover the neurological “magic module” (Merlin Donald) that might explain human language and symbolic thought. The same motivation was still very much present in most twentieth-century research on patients with impaired brains (see, e.g., Geschwind, 1974) or, say, in Chomsky’s battle for the view that the unique properties of human language require a built-in brain device for its generation (contrast Deacon, 1997, who offers an alternative view in which language and the brain coevolve, and Oller, chapter 18 in this volume, for both a critique of the Chomskyan nativist view and a forceful defense of a “self-organizational” alternative). However, the results have been inconclusive at best, if not largely negative:

Every conceivable anatomical comparison has been made between chimpanzees and humans, in the hope of finding the critical structure that explains the gulf between us and our closest relatives. But this has yielded very little. Essentially every structure we can describe in the human brain has an equivalent, or homologue, in the chimpanzee. It is thus virtually certain that our common ancestor five million years ago must also have had the same brain architecture. This in turn implies that no radical modular redesign of the human nervous system has occurred during our evolution. If we are looking for a modular “table of elements” to explain our uniqueness, we had better look somewhere else. It is not there. (Donald, 2001, p. 111)¹³

This caveat having been issued, it seems uncontroversial today that progress in neuroscience, enabled by ever improving anatomical, imaging, and experimental data, has allowed us to identify a number of brain modules at various levels of granularity (e.g., Churchland and Sejnowski, 1992; see also chapters 15 and 16 in this volume). Neuropsychology typically links behavioral data with regions of the brain, using mainly brain-damaged patients and brain-imaging techniques. In this context, Kosslyn and Koenig’s (1992) notion of “weak modularity” is relevant: “Even though

networks compute input–output mappings, the same network may belong to several processing systems; and, while there is a good measure of localization in the brain, it is also often the case that neurons participating in the same computation belong to different regions” (chapter 15 in this volume).

Cognitive Modularity

Although they are much “softer” in comparison to neural accounts of modularity, much more heat has been generated by various *modularity of mind* hypotheses. These originated in the 1980s on a wave of skepticism about the possibility of a “grand design” for different cognitive phenomena (Turner et al., 1997; see also chapter 16 in this volume) on which evolutionary psychologists continue to surf.

Fodor (1983) argued that there are only two major classes of cognitive entities in the brain: (1) domain-specific mental modules, which include the (unconscious) computations underlying vision and our other input systems as well as the output systems that account for behavior (see also Rozin, 1976), and (2) a domain-general (and conscious) central processor that is barred access to the details of whatever modules do (there must be some domain-general “central systems” that interface with the modules; Fodor, 1983, pp. 101–103).

Echoing Chomsky, Fodor thought that language is one of the modules of mind rather than part of the central processor. (One argument for this stance concerns the *involuntary* dimension of the acquisition, generation, and perception of language.) The essence of Fodorian modularity, then, is “information encapsulation”: some of the information outside the module is not accessible from within (Fodor, 1983, p. 71). The restrictions on information flow engender several other symptoms. Modules are “mandatory” (one cannot control whether or not a module applies to a given input); they are typically fast in comparison to nonmodular processes (see Gigerenzer, 1997, and Gigerenzer and Todd, 1999 on “fast and frugal heuristics”); they are “computationally shallow” in that they provide only a preliminary characterization of output; modular mechanisms are associated with fixed neural architecture and, as a consequence, possess characteristic breakdown patterns.

Whereas Fodor’s view, like Chomsky’s, was and remains clearly anti-Darwinian (chapter 14 in this volume), the evolutionary psychologists who radicalized the modularistic stance (e.g., Barkow et al., 1992; see also Carroll, 1988; Garfield, 1991; Hirschfeld and Gelman, 1994; Sperber, 1994, 2002; Charland, 1995; Segal, 1996) and their philosophical associates, such as Steven Pinker (1997), typically embrace the adaptationist reading of the Modern Synthesis due to Williams (1966) and Dawkins (1976). According to their “massive modularity hypothesis” (MMH), the human mind is composed largely, if not entirely, of innate, special-purpose computational

mechanisms or “modules.” (Paradoxical as it may seem for scholars who claim to take evolution seriously, evolutionary psychologists tend to be remarkably silent on the issue of apes-to-humans continuity: Heyes, 2000.) The four central tenets of evolutionary psychology (EP) are (1) *computationalism*: the human mind is an information-processing device that can be likened to “a computer made out of organic components rather than silicon chips” (Cosmides et al., 1992, p. 7); (2) *nativism*: much of the human mind is taken to be innate; (3) *adaptationism*, as suggested above: our minds are the mosaic, evolutionary product (see the Swiss army knife metaphor) of a great number of adaptations to challenges posed by the “environment of evolutionary adaptation” in our Pleistocene past; and (4) *massive modularity*, according to which the human mind contains a (very) large number—hundreds, if not thousands—of “Darwinian modules,” comprising both peripheral systems and central capacities such as reasoning (see Samuels 1998, 2000; Sperber, 2002). Contrary to Fodor, evolutionary psychologists have had little to say about the neural constraints on their cognitive modules (Scholl, 1997; Panksepp and Panksepp, 2000; chapter 16 in this volume).

EP is sometimes presented as simply “psychology that is informed by the additional knowledge that evolutionary biology has to offer” (Cosmides et al., 1992, p. 3). Its advocates suggest that the very existence of modularity and of the specific modules it postulates begs for an evolutionary explanation. They wonder why this is uncontroversial in the case of nonpsychological modular components of the organism (e.g., the liver or the eyes), “which are generally best understood as adaptations” (Sperber, 2002), but raises eyebrows as soon as it comes to psychology. To the extent that EP aims to complete our causal account of mental capacities by including the phylogenetic dimension (the *explanatory* project in Grantham and Nichols’s 1999 terms), it should be rather uncontroversial. As Sperber (2002, p. 49) views it, the evolutionary perspective is especially relevant to psychology, and in particular to the study of cognitive architecture, because *we know so little about the mind*: “Apart from input and output systems, which, being linked to sensory and motor organs, are relatively discernible, there is nothing obvious about the organization of the mind into parts and sub-parts. Therefore all sources of insight and evidence are welcome.”

But EP’s range of usefulness is supposed to extend beyond explaining why we have certain mechanisms once other branches of psychology have discovered them. Its more ambitious goal is to use the tools of evolutionary biology to predict which mechanisms ought to constitute the brain (Grantham and Nichols call this the *predictive* project). Drawing on the theory of natural selection is appealing here because one of its primary objectives is to explain the functional organization of

organisms (see note 1). However, there is no consensus on the kinds of *constraints* evolutionary concepts place on psychological inquiry. The stand one takes on such constraints is formed in large part by how one understands the operation of natural selection. On one account, exemplified by EP *sensu stricto*, selection must produce highly specialized products tailored to fit the specific environmental conditions considered to cause adaptive problems. Consequently, the brain should be composed of a number of dedicated modules, each outfitted to deal with an adaptive problem.

In contrast, Millikan (1993) and Rozin (1976), among others, argue that natural selection *could* produce general-purpose cognitive devices. Dennett's pragmatic view, although in principle closer to EP, ultimately boils down to the same: "Learning is *not* a general-purpose process, but human beings have so many special-purpose gadgets, and learn to harness them with such versatility, that learning *often* can be treated as if it were an entirely medium-neutral and content-neutral gift of non-stupidity" (Dennett, 1995, p. 491). The philosopher Brandon (1990), for one, has suggested that flexible phenotypes prove advantageous in rapidly changing environments whose fluctuations are difficult to predict. Extending this idea to human cognitive evolution, overly specialized devices might not be able to cope with the rapid changes—and, more to the point, natural selection would not have the time to build an array of specialized devices to contend with the conditions.

Inspired in part by connectionism, Karmiloff-Smith (1992) combines a minimal nativism, which she redefines within a "truly epigenetic perspective of genetic expression rather than genetic unfolding," with Piagetian constructivism (Piaget's view was basically antimodularist). She argues that domain-specific predispositions give development "a small but significant kickstart" by focusing the young infant's attention on proprietary inputs. The early period is then followed by intricate interaction with the environment, which crucially affects brain development in return as subsequent learning takes place.

In chapter 14 of this volume, on mind/brain modularity in an evolutionary-connectionist framework, Calabretta and Parisi likewise argue for a form of connectionism that is neither antimodularist nor antinativist. In their discussion of "theory of mind" (ToM)—the (meta)theory of how people or animals attribute mental states to each other and use them to predict others' behavior—Scholl and Leslie (1999) also address the seeming tension between developmental and "static," nondevelopmental, cognitive-modular accounts of ToM. They explore how ToM may be grounded in a cognitive module, yet still afford development, and conclude that a modular capacity such as ToM may be acquired in at least four distinct ways: (1) the innate capacity is fixed but needs to be appropriately triggered in order to develop fully; (2) the essential character of the capacity is determined by

environmental parameter setting; (3) it has an innate basis which is later fixed by module-*internal* development, making use only of information “allowed” past the module’s informational boundaries; and finally (4) some of the properties and contents of the capacity or skill may not have an innate basis at all—the capacity may be “cognitively penetrable” and learnable by induction (see Karmiloff-Smith, 1992). This classification is not necessarily exhaustive. Obviously, much more systematic connectionist modeling and fine-grained neurodevelopmental and neurogenetic evidence will be required to settle this rapprochement.

Closing the Gap Between Mind and Brain

Gobet (chapter 15 in this volume) distinguishes three meanings of modularity in psychology: the biological (see above), the functional (à la Fodor or EP), and the knowledge meaning. The latter refers to the modular organization of knowledge (“representation”) and has some kinship with the notion of modularity used in computer science and artificial intelligence.

Evolutionary psychologists are not always very clear as to where their “Darwinian” modules belong in terms of this threefold distinction. Samuels (2000) usefully distinguishes between “computational” and “Chomskyan” modules. In his terminology, a Chomskyan module is a domain-specific body of mentally represented knowledge or information that accounts for a cognitive capacity, whereas computational modules are specific computational devices. As systems of *representations*, “inert” Chomskyan modules play a role that differs importantly from that of computational modules, which often “manipulate” the former. The “Darwinian modules” of EP are typically domain-specific computational *mechanisms*, and hence not Chomskyan modules in Samuels’ sense.

However, evolutionary psychologists do typically assume that (many) Darwinian modules utilize domain-specific systems of knowledge (i.e., Chomskyan modules). Samuels further distinguishes between strong massive modularity, which assumes that *all* cognitive mechanisms are Darwinian modules in the aforementioned sense, and weak massive modularity, which maintains only that the human mind, including its parts that are responsible for central processing, is *largely* modularly structured. At least some evolutionary psychologists reject the strong MMH in Samuels’ sense.

These distinctions are relevant if one wants to assess the empirical evidence for the role of Darwinian as opposed to just Chomskyan modules in central cognition. ToM is quite generally regarded as “the most well-developed experimental case for a computational or Darwinian module that is not peripheral in character (Samuels, 2000, p. 38). Evidence for a computational ToM module comes mainly from disso-

ciative studies (selective impairment). Thus, Williams syndrome subjects with wide ranges of cognitive impairment typically pass false belief tasks (i.e., tasks evaluating whether or not subjects understand when one might hold a false belief), whereas autistic adolescents and adults with normal IQs typically fail them. However, the available evidence does not allow one to decide in favor of an impaired *computational* ToM module as opposed to a specialized body of ToM *knowledge* (Samuels, 1998).¹⁴ Data from experiments on normal subjects, such as the Wason selection task, are similarly inconclusive. These and similar problems concerning the discrimination between functional (say, Darwinian) modules and knowledge or Chomskyan modules add to the general problem of interrelating mind modules and their neural correlates (Scholl, 1997).

My aim in this introductory chapter has not been to spell out the views of the evolutionary psychologists in any more detail than necessary for a proper understanding of part IV—they are extremely well publicized, especially in the more popular media. Nor is this the place to survey the various lines of criticism that have been addressed to them in addition to those included in this volume (see, among many other sources, Carroll, 1988; Sterelny, 1995; Looren de Jong and van der Steen, 1998; Shapiro and Epstein, 1998; Lloyd, 1999; Buller and Hardcastle, 2000; Fodor, 2000; Panksepp and Panksepp 2000, 2001; Rose and Rose, 2000). Just one final remark: Wagner et al. (chapter 2 in this volume), in their discussion of the origin of modularity, point to “mechanistic plurality” as a real possibility. Maybe taking this message to heart can alleviate the frustration of those among us who feel that too much arbitrariness is involved in the current evolutionary-psychological debates.

Acknowledgments

I am grateful to my coeditor Diego Rasskin-Gutman for carefully commenting on the draft version of this chapter. Although I did my best to take his advice to heart wherever I could endorse it, the tension between his Platonist *weltanschauung* and my more down-to-earth naturalistic philosophy of science remains considerable, so that I cannot humanly expect him to embrace the final product. Our conversation will thus have to be continued. Meanwhile, I have to take full responsibility for any remaining imbalances or worse errors. I also thank James Phelps, whose thoughtful interpretation of the program of EP has inspired some of the views expounded in the section on cognitive and neural modularity, and Sahotra Sarkar for allowing me to read parts of an unpublished book manuscript on evolution from a developmental point of view.

Notes

1. According to Simon (1969, pp. 5–6), artificial things “are synthesized (though not always or usually with full forethought) by man”; they “may imitate appearances in natural things while lacking, in one or many respects, the reality of the latter”; they “can be characterized in terms of functions, goals, adaptation”; and they “are often discussed, particularly when they are being designed, in terms of imperatives as well as descriptives.” An important fact about functional explanation, Simon specified, is that it demands an understanding mainly of the outer environment (see Godfrey-Smith, 1996). “Analogous to the role played by natural selection in evolutionary biology is the role played by rationality in the sciences of human behavior. If we know of a business organization only that it is a profit-maximizing system, we can often predict how its behavior will change if we change its environment. . . . We can make this prediction . . . without any detailed assumptions about the adaptive mechanisms, the decision-making apparatus that constitutes the inner environment of the business firm” (Simon, 1969, p. 8). At the most general level, Simon (1973, p. 3) maintained, there are properties related to hierarchy that are “common to a very broad class of complex systems, independently of whether those systems are physical, chemical, biological, social, or artificial. The existence of these commonalities is a matter of empirical observation; their explanation is, in a broad sense, Darwinian—they concern properties that facilitate the evolution and survival of complexity.”
2. See, e.g., Hall (1992); Gilbert et al. (1996); the editorial by Raff et al. (1999) in the first issue of the journal *Evolution and Development*; Müller and Newman (2003); and Robert (2004).
3. See, e.g., Dennett (1995); David (2000); and Langlois and Savage (2001). See also Wagner and Altenberg (1996); Wagner et al. (chapter 2 in this volume); and Marengo et al. (chapter 17 in this volume) on decomposability in genetic algorithms.
4. In their work on the heuristics used in both original scientific discovery and novice learning, Simon and his coworkers have shown that calculations such as these can quite easily be automated; see in particular Simon (1977a); Simon et al. (1981); and Langley et al. (1987) on the BACON programs.
5. Supposing that the more exact a system’s description is, the more complex it is, one could say that the inherent complexity of an object in principle constitutes the floor for the complexity of an exact description.
6. Although on some of its interpretations, modularity comes conceptually close to Simon’s concept of near decomposability of hierarchical systems (e.g., chapter 15 in this volume), hierarchy does not conceptually imply modularity. Thus Simon’s (1969) original example of rooms connected by corridors shows a modular design but no hierarchy. In biology this is even more evident: a molecule with different domains shows modularity, but not hierarchy (the hierarchy here is manifested differently, as linear chain → secondary and tertiary structure). The limb is modular, but there is no hierarchy of bones; in this case the hierarchy is one of molecules-cells-tissues, etc. (Diego Rasskin-Gutman, personal communication; see also Agre, 2003). Yet many of the complex systems we encounter, whether assembled from diverse smaller components or through specialization of identical or similar units, display a ND structure (Simon, foreword to this volume) *and* do happen to be modular as well (e.g., Blume and Appel, 1999, and chapters 2 and 11 in this volume). Simon’s suggestion that *any* complex, naturally evolved system is constituted by a decomposable hierarchy is challenged by Zawidzki (1998), who takes Kauffman’s (1993) models of genetic regulatory networks to provide counterexamples.
7. Not without irony, the experimental work reported in Atran (1998) “supports a modular view of folk biology as a core domain of human knowledge.”
8. In the conclusion of his *Inductive Inference and Its Natural Ground*, Hilary Kornblith has this to say on the human ability to cope with natural kinds: “[W]e are quite adept at detecting the very features of natural kinds which are essential to them, and our conceptual structure places these essential features in the position of driving inductive inference. . . . [W]e typically project the properties of natural kinds which are universally shared by their members. It is thus that our inductive inferences are tailored to the causal structure of the world, and thus that inductive understanding of the world is possible” (Kornblith, 1995, p. 107).

9. An important question in this context, which can only be mentioned here, concerns the nature of the “glue” that holds the components of a system together. In Simon’s example of the solar system, the “distributional facts” remain unexplained; they call for further explanation beyond the Newtonian framework, possibly in the realm of cosmogony. In living systems—especially if one is interested in their origination (Müller and Newman, 2003)—physical (as well as chemical) *forces* that vary with distance continue to be important *explanantia* of form. But as soon as some sort of *scarce energy* enters the scene, the issue of differential allocation arises (Marengo et al., chapter 17 in this volume). Here Simon’s (1969) evolutionary argument of the two watchmakers would seem to gain its full force.
10. Additional conceptual distinctions are provided in Bolker (2000) and Winther (2001).
11. As Brandon (1990) argues, by avoiding the ecological process of selection, genic selectionism—the idea that all of evolution can be understood in terms of selection acting at the level of genes (Williams, 1966; Dawkins, 1976)—cannot possibly explain what makes an adaptation adaptive. The reasons why modern *developmental* biology has come to ignore the environment ultimately can be traced back to Weismann’s influential proposal that development was merely the segregation of entities residing within the nucleus (Gilbert and Bolker, 2003, p. 4).
12. West-Eberhard (1998, p. 8417) relates this suppression to the opposition between Darwin’s gradualism and the saltationist views that developmental biologists have continued to hold: “The large variants sometimes produced by development . . . invite explanation of adaptive form in terms of accident or divine creation. Darwin was uncompromising on this point and cleverly explained developmentally mediated heterochrony as involving complex traits first established by gradual change in ancestral juveniles or adults. . . .”
13. Donald acknowledges Terry Deacon’s claim that in humans, certain parts of the frontal cortex expanded considerably and extended their range of interconnections over evolutionary time (see Deacon, 1997). But he considers this a quibble over small facts, insisting that “The Big Fact is one that should be inscribed on every cognitive theorist’s door: NO NEW MODULES” (2001, p. 112).
14. Connectionist neuropsychology poses additional problems for modularists invoking dissociation; see, e.g., Plaut (1995).

References

- Adami C (2002) Ab initio modeling of ecosystems with Artificial Life. *Nat Res Model* 15: 133–145.
- Agre PE (2003) Hierarchy and history in Simon’s “Architecture of complexity.” *J Learn Sci* 12: 413–426.
- Amundson R (1994) Two concepts of constraint: Adaptationism and the challenge from developmental biology. *Phil Sci* 61: 556–578.
- Atran S (1998) Folk biology and the anthropology of science: Cognitive universals and cultural particulars. *Behav Brain Sci* 21: 547–609.
- Baldwin CY, Clark KB (1997) Managing in an age of modularity. *Harvard Bus Rev* 75(5): 84–93.
- Barbuti R, Giacobazzi R, Levi G (1993) A general framework for semantics based on bottom-up abstract interpretation of logic programs. *ACM Trans Program Lang Sys* 15(1): 133–181.
- Barkow JH, Cosmides L, Tooby J (eds) (1992) *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. New York: Oxford University Press.
- Barrett HC (2001) On the functional origins of essentialism. *Mind Soc* 2: 1–30.
- Bechtel W, Richardson RC (1993) *Discovering Complexity: Decomposition and Localization as Strategies in Scientific Research*. Princeton, NJ: Princeton University Press.
- Blume M, Appel AW (1999) Hierarchical modularity. *ACM Trans Program Lang Systems* 21: 513–547.
- Bolker JA (2000) Modularity in development and why it matters to Evo-Devo. *Amer Zool* 40: 770–776.

- Bonner JT (1988) *The Evolution of Complexity by Means of Natural Selection*. Princeton, NJ: Princeton University Press.
- Brandon RN (1990) *Adaptation and Environment*. Princeton, NJ: Princeton University Press.
- Brandon RN (1999) The units of selection revisited: The modules of selection. *Biol Philos* 14: 167–180.
- Brooks RA (1997) Intelligence without representation. In: *Mind Design II* (Haugeland J, ed), 395–420. Cambridge, MA: MIT Press.
- Buller DJ, Hardcastle VG (2000) Evolutionary psychology meets developmental neurobiology: Against promiscuous modularity. *Mind Brain* 1: 307–325.
- Callebaut W (1989) Post-positivist views of scientific explanation. In: *Explanation in the Social Sciences: The Search for Causes in Demography* (Duchêne J, Wunsch G, Vilquin E, eds), 141–196. Brussels: Ciaco.
- Callebaut W (1995) Réduction et explication mécaniste en biologie. *Rev Philos Louvain* 91: 33–66.
- Callebaut W, Stotz K (1998) Lean evolutionary epistemology. *Evol Cognit* 4: 11–36.
- Carroll, JM (1988) Modularity and naturalness in cognitive science. *Metaphor Symbol Activ* 3(2): 61–86.
- Charland L (1995) Feeling and representing: Computational theory and the modularity of affect. *Synthese* 105: 273–301.
- Churchland PS, Sejnowski TJ (1992) *The Computational Brain*. Cambridge, MA: MIT Press.
- Conrad M (1990) The geometry of evolution. *BioSystems* 24: 61–81.
- Cosmides L, Tooby J, Barkow JH (1992) Introduction: Evolutionary psychology and conceptual integration. In: *The Adapted Mind* (Barkow JH, Cosmides L, Tooby J, eds), 3–15. New York: Oxford University Press.
- David, PA (2000) Path dependence and varieties of learning in the evolution of technological practice. In: *Technological Innovation as an Evolutionary Process* (Ziman J, ed), 118–133. Cambridge: Cambridge University Press.
- Dawkins R (1976) *The Selfish Gene*. Oxford: Oxford University Press.
- Dawkins R (1996) *Climbing Mount Improbable*. New York: Norton.
- Deacon TW (1997) *The Symbolic Species: The Co-evolution of Language and the Brain*. New York: Norton.
- Dennett DC (1995) *Darwin's Dangerous Idea: Evolution and the Meanings of Life*. New York: Simon & Schuster.
- Donald M (2001) *A Mind So Rare: The Evolution of Human Consciousness*. New York: Norton.
- Fodor JA (1983) *The Modularity of Mind: An Essay on Faculty Psychology*. Cambridge, MA: MIT Press.
- Fodor JA (2000) *The Mind Doesn't Work That Way: The Scope and Limits of Computational Psychology*. Cambridge, MA: MIT Press.
- Fontana W, Buss LW (1994) “The arrival of the fittest”: Toward a theory of biological organization. *Bull Math Biol* 56: 1–64.
- Garfield, JL (1991) *Modularity in Knowledge Representation and Natural-Language Understanding*. Cambridge, MA: MIT Press.
- Gerhart J, Kirschner M (1998) Evolvability. *Proc Natl Acad Sci USA* 95: 8420–8427.
- Geschwind N (1974) *Selected Papers on Language and the Brain*. Dordrecht: Reidel.
- Gigerenzer G (1997) The modularity of social intelligence. In: *Machiavellian Intelligence II: Extensions and Evaluations* (Byrne RW, Whiten A, eds), 264–288. Cambridge: Cambridge University Press.
- Gigerenzer G, Todd PM (eds) (1999) *Simple Heuristics That Make Us Smart*. New York: Oxford University Press.
- Gilbert SF, Bolker JA (2001) Homologies of process and modular elements of embryonic construction. *J Exp Zool (Mol Dev Evol)* 291: 1–12.

- Gilbert SF, Bolker JA (2003) Ecological developmental biology: Preface to the symposium. *Evol Dev* 5(1): 3–8.
- Gilbert SF, Opitz JM, Raff RA (1996) Resynthesizing evolutionary and developmental biology. *Dev Biol* 173: 357–372.
- Godfrey-Smith P (1996) *Complexity and the Function of Mind in Nature*. Cambridge: Cambridge University Press.
- Grantham TA, Nichols S (1999) Evolutionary psychology: Ultimate explanations and Panglossian predictions. In: *Where Biology Meets Psychology: Philosophical Essays* (Hardcastle VG, ed), 47–66. Cambridge, MA: MIT Press.
- Griesemer JR (2002) What is “epi” about epigenetics? In: *From Epigenesis to Epigenetics: The Genome in Context* (Van Speybroeck L, Van de Vijver G, De Waele D, eds), *Ann NY Acad Sci* 981: 97–110.
- Griffiths PE, Gray RD (2001) Darwinism and developmental systems. In: *Cycles of Contingency: Developmental Systems and Evolution* (Oyama S, Griffiths PE, Gray RD, eds), 195–218. Cambridge, MA: MIT Press.
- Hall BK (1992) *Evolutionary Developmental Biology*. London: Chapman and Hall.
- Hansen TF (2003) Is modularity necessary for evolvability? Remarks on the relationship between pleiotropy and evolvability. *BioSystems* 69: 83–94.
- Heyes CM (2000) Evolutionary psychology in the round. In: *Evolution of Cognition* (Heyes CM, Huber L, eds), 1–21. Cambridge, MA: MIT Press.
- Hirschfeld LA, Gelman SA (eds) (1994) *Mapping the Mind: Domain Specificity in Cognition and Culture*. New York: Cambridge University Press.
- Hull DL (1988) *Science as a Process: An Evolutionary Account of the Social and Conceptual Development of Science*. Chicago: University of Chicago Press.
- Hurley SL (1999) Rationality, democracy, and leaky boundaries: Vertical vs. horizontal modularity. In: *Democracy's Edges* (Shapiro I, Hacker-Cordón C, eds), 273–294. Cambridge: Cambridge University Press.
- Husken M, Igel C, Toussaint M (2002) Task-dependent evolution of modularity in neural networks. *Connect Sci* 14: 219–229.
- Jablonka E (2001) The systems of inheritance. In: *Cycles of Contingency: Developmental Systems and Evolution* (Oyama S, Griffiths PE, Gray RD, eds), 99–116. Cambridge, MA: MIT Press.
- Karmiloff-Smith A (1992) *Beyond Modularity: A Developmental Perspective on Cognitive Science*. Cambridge, MA: MIT Press.
- Kauffman S (1993) *The Origins of Order*. Oxford: Oxford University Press.
- Kitcher P (2001) Battling the undead: How (and how not) to resist genetic determinism. In: *Thinking About Evolution: Historical, Philosophical, and Political Perspectives* (Singh RS, Krimbas CB, Paul DB, Beatty J, eds), 396–414. New York: Cambridge University Press.
- Kornblith H (1995) *Inductive Inference and Its Natural Ground: An Essay in Naturalistic Epistemology*. Cambridge, MA: MIT Press.
- Kosslyn SM, Koenig O (1992) *Wet Mind*. New York: Free Press.
- Langley P, Simon HA, Bradshaw GL, Zytkow JM (1987) *Scientific Discovery: Computational Explorations of the Creative Processes*. Cambridge, MA: MIT Press.
- Langlois RN, Savage DA (2001) Standards, modularity, and innovation: The case of medical practice. In: *Path Dependence and Creation* (Garud R, Karnøe P, eds), 149–168. Mahwah, NJ: Lawrence Erlbaum.
- Levinson P (1982) Evolutionary epistemology without limits. *Knowl: Creat, Diff, Util* 4: 465–502.
- Lewontin RC (1974) *The Genetic Basis of Evolutionary Change*. New York: Columbia University Press.
- Lloyd EA (1999) Evolutionary psychology: The burdens of proof. *Biol Philos* 14: 211–233.

- Looren de Jong H, Van der Steen WJ (1998) Biological thinking in evolutionary psychology: Rockbottom or quicksand? *Phil Psych* 11: 183–205.
- Millikan RG (1993) *White Queen Psychology and Other Essays for Alice*. Cambridge, MA: MIT Press.
- Minelli A (1998) Molecules, developmental modules, and phenotypes: A combinatorial approach to homology. *Molec Phylogenet Evol* 9: 340–347.
- Moss L (2001) Deconstructing the gene and reconstructing molecular developmental systems. In: *Cycles of Contingency: Developmental Systems and Evolution* (Oyama S, Griffiths PE, Gray RD, eds), 85–97. Cambridge, MA: MIT Press.
- Moss L (2003) *What Genes Can't Do*. Cambridge, MA: MIT Press.
- Müller GB, Newman SA, eds (2003) *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology*. Cambridge, MA: MIT Press.
- Müller GB, Olsson L (2003) Epigenesis and epigenetics. In: *Keywords in Evolutionary Developmental Biology* (Hall BK, Olson W, eds), 114–123. Cambridge, MA: Harvard University Press.
- Müller GB, Wagner GP (1996) Homology, Hox genes, and developmental integration. *Amer Zool* 36: 4–13.
- Needham J (1933) On the dissociability of the fundamental processes in ontogenesis. *Biol Rev* 8: 180–223.
- Newman SA, Müller GB (2000) Epigenetic mechanisms of character organization. *J Exp Zool (Mol Dev Evol)* 288: 304–317.
- Oyama S, Griffiths PE, Gray RD (2001) Introduction: What is Developmental Systems Theory? In: *Cycles of Contingency: Developmental Systems and Evolution* (Oyama S, Griffiths PE, Gray RD, eds), 1–11. Cambridge, MA: MIT Press.
- Panksepp J, Panksepp JB (2000) The seven sins of evolutionary psychology. *Evol Cognit* 6: 108–131.
- Panksepp J, Panksepp JB (2001) A continuing critique of evolutionary psychology: Seven sins for seven sinners, plus or minus two. *Evol Cognit* 7: 56–80.
- Pinker S (1997) *How the Mind Works*. London: Penguin.
- Plaut DC (1995) Double dissociation without modularity: Evidence from connectionist neuropsychology. *J Clin Exp Neuropsychol* 17: 291–321.
- Raff EC, Raff RA (2000) Dissociability, modularity, evolvability. *Evol Dev* 2(5): 235–237.
- Raff RA (1996) *The Shape of Life*. Chicago: University of Chicago Press.
- Raff RA, Arthur W, Carroll SB, Coates MI, Wray G (1999) Editorial: Chronicling the birth of a discipline. *Evol Dev* 1: 1–2.
- Ridley M (1993) *Evolution*. Boston: Blackwell Scientific.
- Riedl RJ (1978) *Order in Living Organisms: A Systems Analysis of Evolution* (Jefferies RPS, trans). New York: Wiley. German orig. 1975.
- Robert JS (2004) *Embryology, Epigenesis, and Evolution: Taking Development Seriously*. Cambridge: Cambridge University Press.
- Robert JS, Hall BK, Olson WM (2001) Bridging the gap between developmental systems theory and evolutionary developmental biology. *BioEssays* 23: 1–9.
- Rose H, Rose S, eds (2000) *Alas, Poor Darwin: Arguments Against Evolutionary Psychology*. New York: Harmony Books.
- Rozin P (1976) The evolution of intelligence and access to the cognitive unconscious. In: *Progress in Psychology* vol. 6, (Sprague JM, Epstein AN, eds), 245–280. New York: Academic Press.
- Samuels R (1998) Evolutionary psychology and the massive modularity hypothesis. *Brit J Phil Sci* 49: 575–602.
- Samuels R (2000) Massively modular minds: Evolutionary psychology and cognitive architecture. In: *Evolution and the Human Mind: Modularity, Language and Meta-Cognition* (Carruthers P, Chamberlain A, eds), 13–46. Cambridge: Cambridge University Press.

- Samuels R, Stich S, Tremoulet P (1999) Rethinking rationality: From bleak implications to Darwinian modules. In: *What Is Cognitive Science?* (Lepore E, Pylyshyn Z, eds), 74–120. Oxford: Blackwell.
- Schank JC, Wimsatt WC (1988) Generative entrenchment and evolution. In: *PSA 1986*, vol. 2 (Fine A, Machamer PK, eds), 33–60. East Lansing, MI: Philosophy of Science Association.
- Schank JC, Wimsatt WC (2001) Evolvability, adaptation and modularity. In: *Thinking About Evolution*, vol. 2: Historical, Philosophical, and Political Perspectives (Singh RS, Krimbas CB, Paul DB, Beatty J, eds), 322–335. New York: Cambridge University Press.
- Scholl BJ (1997) Neural constraints on cognitive modularity? *Behav Brain Sci* 20: 575–576.
- Scholl BJ, Leslie AM (1999) Modularity, development and “theory of mind”. *Mind Lang* 14: 131–153.
- Segal G (1996) The modularity theory of minds. In: *Theories of Theories of Mind* (Carruthers P, Smith PK, eds), 141–157. Cambridge: Cambridge University Press.
- Shapere D (1984) *Reason and the Search for Knowledge: Investigations in the Philosophy of Science*. Dordrecht: Reidel.
- Shapiro L, Epstein W (1998) Evolutionary theory meets cognitive psychology: A more selective perspective. *Mind Lang* 13: 171–194.
- Simon HA (1969) *The Sciences of the Artificial*. Cambridge, MA: MIT Press. 2nd ed.
- Simon HA (1973) The organization of complex systems. In: *Hierarchy Theory* (Pattee HH, ed), 3–27. New York: Braziller.
- Simon HA (1977a) *Models of Discovery*. Dordrecht: Reidel.
- Simon HA (1977b) How complex are complex systems? In: *PSA 1976* (Suppe F, Asquith PD, eds), 507–522. East Lansing, MI: Philosophy of Science Association.
- Simon HA (1995) Near decomposability and complexity: How a mind resides in a brain. In: *Mind, the Brain, and Complex Adaptive Systems* (Morowitz HJ, Singer JL, eds), 25–44. Santa Fe Institute Studies in the Sciences of Complexity, Proceedings vol. 22. Reading, MA: Addison-Wesley.
- Simon HA, Langley P, Bradshaw G (1981) Scientific discovery as problem solving. *Synthese* 47: 1–27.
- Sperber D (1994) The modularity of thought and the epidemiology of representations. In: *Mapping the Mind: Domain Specificity in Cognition and Culture* (Hirschfeld LA, Gelman SA, eds), 39–67. New York: Cambridge University Press.
- Sperber D, ed (2000) *Metarepresentations: A Multidisciplinary Perspective*. New York: Oxford University Press.
- Sperber D (2002) In defense of massive modularity. In: *Language, Brain and Cognitive Development. Essays in Honor of Jacques Mehler* (Dupoux E, ed), 47–57. Cambridge, MA: MIT Press.
- Star LS (1989) *Regions of the Mind: Brain Research and the Quest for Scientific Certainty*. Stanford, CR: Stanford University Press.
- Sterelny K (1995) Review of (Barkow et al. 1992). *Biol Psychol* 10: 365–380.
- Sterelny K (2001) Niche construction, developmental systems, and the extended replicator. In: *Cycles of Contingency: Developmental Systems and Evolution* (Oyama S, Griffiths PE, Gray RD, eds), 333–349. Cambridge, MA: MIT Press.
- Székelly G (2001) An approach to the complexity of the brain. *Brain Res Bull* 55(1): 11–28.
- Turner JH, Borgerhoff Mulder M, Cosmides L, Giesen B, Hodgson G, Maryanski AM, Shennan SJ, Tooby J, Velichkovsky BM (1997) Looking back: Historical and theoretical context of present practice. In: *Human by Nature: Between Biology and the Social Sciences* (Weingart P, Mitchell SD, Richerson PJ, Maasen S, eds), 17–64. Mahwah, NJ: Erlbaum.
- Von Dassow G, Munro E (1999) Modularity in animal development and evolution: Elements of a conceptual framework for EvoDevo. *J Exp Zool (Mol Dev Evol)* 285: 307–325.
- Wagner GP (1995) The biological role of homologues: A building block hypothesis. *N Jb Geol Paläont Abh* 195: 279–288.

- Wagner GP (1996) Homologues, natural kinds, and the evolution of modularity. *Amer Zool* 36: 36–43.
- Wagner GP, Altenberg L (1996) Perspective: Complex adaptations and the evolution of evolvability. *Evolution* 50: 967–976.
- Wagner GP, Laubichler MD (2000) Character identification in evolutionary biology: The role of the organism. *Theory Biosci* 119: 20–40.
- Wagner GP, Laubichler MD (2004) Rupert Riedl and the re-synthesis of evolutionary and developmental biology: Body plans and evolvability. *J Exp Zool (Mol Dev Evol)* 302B: 92–102.
- West-Eberhard MJ (1998) Evolution in the light of developmental and cell biology, and vice versa. *Proc Natl Acad Sci USA* 95: 8417–8419.
- Wheeler M, Clark A (1999) Genic representation: Reconciling content and causal complexity. *Brit J Phil Sci* 50: 103–135.
- Williams GC (1966) *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.
- Wimsatt WC, Schank JC (1988) Two constraints on the evolution of complex adaptations and the means of their avoidance. In: *Evolutionary Progress* (Nitecki MH, ed), 231–275. Chicago: University of Chicago Press.
- Winther RG (2001) Varieties of modules: Kinds, levels, origins and behaviors. *J Exp Zool (Mol Dev Evol)* 291: 116–129.
- Zawidzki TW (1998) Competing models of stability in complex, evolving systems: Kauffman vs. Simon. *Biol Phil* 13: 541–554.