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MODULARITY: UNDERSTANDING THE DEVELOPMENT AND EVOLUTION OF COMPLEX NATURAL SYSTEMS

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The topic

The success of modern science largely depends on the elaboration and investigation of simple systems, whether natural or artificial, as a reflection of the complexity of the actual ones. In general, the number of conceivable interactions among parts (say, the number of logically or even physically possible interactions) largely exceeds the number of interactions that must actually be taken into account to yield system descriptions that are realistic enough. This happy condition was critical for the articulation of classical mechanics, the paradigmatic science of simplicity ("If the deck of cards that Nature dealt to KEPLER and NEWTON was not stacked, it was at least a very lucky deal" - Herbert A. SIMON). But it also extends, albeit less spectacularly, to the complex systems that scientists and engineers are at present learning to handle.

In the latter case, the possibility of scientific understanding would seem to crucially depend on the modular character of the "(nearly) decomposable systems" (SIMON) one is interested in. Decomposition allows the subdivision of the explanatory task into manageable chunks. A decomposable system is modular in that each component or module operates primarily according to its own, intrinsically determined principles. Each component is dependent at most upon inputs from other components, influences other components only by itsoutputs, and has a specific, intrinsic function. For instance, in the case of biological evolution, a module of selection may be regarded as a set of genes, their products and interactions (their developmental pathways), the resulting character complex, and the functional effect of that complex. The primary function of the module is phenotypic selection - an ecological process. The genes affecting the character complex serving the ecological function must have a high degree of internal integration and a low degree of external connectivity (pleiotropic connections must largely be within-module). For BRANDON (1999a) following WAGNER and ALTENBERG (1996), such modules are the true units of selection.

Thinking in terms of modularity has quite an impressive track record in biology and psychology including, e.g., GALL's phrenology, 19th and 20th century debates in physiology and genetics, or Leibniz' monadology. At present, the existence of modules is recognized at all levels of biological organization (CALABRETTA et al. 1996). Also, it has been claimed that modularity can be precisely defined in terms of a biophysically grounded model of a genotype-phenotype map (ANCEL and FONTANA 1999). Modularity is a central concept in both the neurosciences and computer science. In cognitive science, a lively debate on the topic was occasioned by FODOR's The Modularity of Mind (1983), and an entire new discipline, evolutionary psychology, is grounded on the "swiss army knife" model of perception and cognition.

We think the time is ripe to bring together experts in the fields of developmental and evolutionary biology, artificial life, the neuro- and the cognitive sciences, and systems theory, to try to bring about a useful knowledge transfer between these diverse disciplines. As a general goal the workshop will try to clarify what modules are, why and how they emerge and change, and what this implies for our respective research agendas.

In a way, the current situation looks paradoxical:

* One cluster of scientists - roughly, those working in the cognitive field, have invested considerably in the symbolic-computational paradigm for the study of mind. As the field has begun to converge on computationalism, several rather fundamental methodological conflicts, threatening its coherence, have become discernible. They have to do mainly with assumptions about the modular structure of the mind

and, accordingly, about what constitute natural cognitive domains for scientific analysis (e.g., HENDRIKS-JANSEN 1996). While hotly debating the pros and cons of conceiving the (human) brain/mind in terms of modularity, 'cognitivists' (and to a lesser extent neuroscientists) have not usually been very clear about its very definition and operationalization (as we witnessed at the closing session of the Third Altenberg Workshop in Theoretical Biology.)

* On the other hand, other researchers - roughly, those in the biological camp, including systems theorists - do seem to possess 'workable' modularity concepts, but with few exceptions fail to see a need to rethink (part of) their research agenda in terms of modularity (but see BRANDON 1999).

In addition to being beneficial to both groups per se, the workshop could foster a better understanding of the modalities of multi- and interdisciplinary collaboration in a 'post-reductionist' setting, reviving an old ambition of Systems Theory and, hence, Theoretical Biology. In a sense, modularity can be viewed as the nexus towards the elaboration of a naturalist account of the world. Where wholism and system theories have failed, modularity might be destined to find its way as the ultimate descriptive tool in natural sciences.

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Abstracts

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Selection for Modularity in the Genome

Modularity in the organization of the genome poses a problem for Darwinian theory because it is not a phenotype of the organism, but rather a variational property defining the possibilities for change. I describe how selection can act on the possibilities for change through change itself: during the creation of new genes. Because new genes are the source for the degrees of freedom of the genome, selection on new genes also selects on the degrees of freedom. New genes must advance adaptation while not perturbing existing adaptations in order to be preserved by selection. This selects for a specific kind of modularity in the genotype-phenotype map, and enhances the ability of both allelic variation and genome growth to produce adaptations. Structural manifestations of this process are evidenced in the reading frame properties of exons, and the proliferation of functional and regulatory modules in the genome. The dynamics of this `constructional selection' process can be modeled and quantitative predictions made about its efficacy, relation to genome size, and macroevolutionary consequences.

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Evolutionary Origins of Modularity in RNA Structure

The evolutionary potential of a population fundamentally depends on the production of novel phenotypes through mutation and recombination. Viruses that evolve quickly to outmaneuver host immunity, for example, must readily access genetic variation with functional consequences. Waddington introduced the term "genetic canalization" to describe the robustness of a phenotype in the face of random genetic changes. Taken to an extreme, genetic canalization may preclude the phenotypic innovation that fuels evolution. The environmental counterpart to genetic canalization is "environmental canalization" — the evolution of developmental pathways to withstand chance events in the environment. The folding of RNA sequences into secondary structures provides a simple molecular model for these concepts.

Motivated by an experimental protocol in which RNA sequences are evolved to optimally bind a ligand, we computationally subject RNA sequences to natural selection directed toward a optimal molecular structure. I will describe the three surprising outcomes of our analysis:
1. Genetic canalization and environmental canalization share a common biophysical basis.
2. Extreme genetic canalization, to the point of an evolutionary dead-end, is produced as a side effect of environmental canalization.
3. The hallmark of canalized phenotypes is modularity.

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The Modules of Selection

The talk will be divided into four parts. First I review the old "units" or "levels" of selection problem. This is an area in which there has been fruitful collaboration between philosophers of biology and theoretical biologists. Next I review some precursors of contemporary work on modularity, in particular Lewontin's notion of quasi-independence and Bonner's notion of gene nets. In the third part I offer a characterization of evolutionary/developmental modules. I argue that there are two necessary aspects of such modules: (1) unitary ecological function; and (2) integrated developmental architecture. In the final part I demarcate three types of evidence for the existence of evolutionary/developmental modules. The first is a sort of transcendental argument that adaptive evolution requires such modules. The second is a sort of retrospective evidence from phylogeny—the fact that certain homologous traits have evolved in a modular fashion. The third comes from direct knowledge of developmental architecture and functional integration. This third sort is in many ways the most satisfying, but unfortunately, the most difficult to acquire.

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Modularity: A Performance on the Edge Between Art and Science

Science and art are the two paths of knowledge of human beings. Both science and modern art "-isms" use the concepts of modelling, partitioning, and integration to capture the organisational properties of natural and artificial objects. We do not immediately see modularity in artworks, landscapes, animals, or physical processes. Rather, we have to make a conscious effort to unveil the modular structure of these natural and artificial objects. The choice and definition of “module” is the first elusive issue of this analytical task. But some commonalties are apparent: Every modular system contains a set of discrete connected modules that build up an organised "whole". Furthermore, modules are real entities, e.g., a frequency, a shape, or a human being.

We explore questions that we believe can get us closer to the concept of modularity: How can space be enclosed? How can items be economically ordered or packed? Why do some entities become functionally integrated? What does it mean to grow regularly? How can actions be captured across time? What is the dialectic interplay between order and chaos? Part of the answer to all these questions resides in the fact that, in order to build a modular system, transformations and generative rules are needed. Modern Art provides a perfect pool of examples to explore these questions.

In our conception, modularity emerges dynamically, as a growing system that evolves, which causes modular systems to show emergent properties. Many questions will arise during this performance, but our primary goal is to enjoy a modular show, a journey of images and music.

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Artificial Life Models for Understanding the Evolution of Modularity

The concept of modularity is used with different meanings and implications in several research fields such as cognitive science, evolutionary psychology, neuroscience and robotics. In this paper we start by reviewing these meanings and implications. Then, we claim that the lack of cross-fertilization among these research fields can be overcome by using the simulative models of Artificial Life, in which the presence of the different levels of biological organization forces us to use a common terminology and to elaborate unitary theories which are able to answer the questions asked in different areas. We conclude by presenting some specific examples of simulative models of Artificial Life already successfully used for exploring some open questions in evolutionary biology and cognitive science.

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The Ubiquity of Modularity

It seems fair to say that contemporary thinking about modularity in the sciences (whether or not it comes under this name) is characterized by a double paradox. Researchers in the cognitive sciences, while vigorously debating the pros and cons of conceiving the human brain/mind in terms of modularity and domain-specificity, have not been very clear, generally speaking, about the definition and operationalization of modularity, and even less so about the mechanisms of modularization that any plausible epigenetic perspective will likely require. Some biologists and systems theorists, on the other hand, do possess workable modularity concepts; but with a few notable exceptions – which are well represented at this workshop – they have not felt the need to rethink (part of) their research agendas in terms of "modular foundations".

I will suggest directions for a profitable knowledge transfer between approaches to modularity in a number of disciplines, and discuss the prospects of Simon's pioneering work on nearly decomposable systems for a unified approach to modularity in the cognitive and life sciences.

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Morphological Modularity: An Integrative Approach

Modularity can be characterized, measured, and modeled at several levels in the biological hierarchy. Different levels may express modularity in different ways, on the one hand demanding level-specific definitions, and on the other revealing phenomena unique to particular spatial and temporal scales. It is our contention that while a unified notion of modularity is highly desirable, different operational definitions of modularity may be necessary to allow its fruitful application to various organizational levels. Here we explore the unique problems surrounding morphological modularity in its theoretical and empirical dimensions.

The characterization and study of morphological modules in their own right does not reduce the importance of an understanding of their developmental causation, nor does it reduce the value of ultimately expressing morphological modules as developmental modules. It simply recuperates the ontological semi-independence of morphology in evolution. The reference space of morphological variation then becomes a legitimate target of explanation, to which developmental modules relate necessarily but not sufficiently. The advantage of the reification of morphological modularity is that it can be directly studied in the fossil record, thus allowing a direct window into the evolution of modularity; it can be directly interpreted in terms of classification and systematization; and it can be interpreted in terms of the economic, functional roles that whole organisms and their modules perform in ecological assemblages.

Theoretically, morphological modularity brings the need for models and abstractions that can appropriately capture both the organization and the complexity of organisms. The concept of morphospace provides an appropriate framework to analyze modularity as a topological property of form, with four levels of description: proportions, orientations, connections and articulations. These levels are adequate and operationally sufficient to provide a full description of organic form. Although geometric models of growth have occupied a central position in theoretical morphology, the modeling and construction of morphospaces where modularity per se is embedded may benefit from hitherto unexplored approaches, such as graph theory and cellular automata. A further task of the theoretical approach to morphological modularity is to locate the placement within morphospace theory of macroevolutionary aspects such as disparity, diversity, homology, etc.

Empirically, the proper study of morphological modularity demands rigorous methods of description and representation of form, as well as statistical criteria for the decomposition of wholes into parts and for the definition of classes of autonomous behavior. Autonomous behavior in turn is reflected in the ability of a part, or module, to change in relative independence from other parts. This invites the use of multivariate statistical methods for the decomposition of variation into statistically independent components, or of statistical tests of a priori hypotheses of modularity. While such approaches do not mechanistically justify the definition of modules, they may help in their characterization, to the extent that organizational independence is correlated with variational independence. In macroevolution, where the focus is on interspecific evolution, disparity becomes a reference quantity in the study of variational properties through time. While raw disparity data are measuring variation only, it can often be decomposed into contributions likely to reflect variability (variational potential). Examples of the possible connections between disparity and modularity are provided.

We conclude by stressing that it is precisely the dialectic interplay of possibilities within theoretical morphospace and actual realizations in empirical morphospace that creates a domain for the operational definition of morphological modules (and nonmodules) as well as for the interpretation of their changes in evolutionary terms. The proposed integration of morphological data within the framework provided by morphospace theory should facilitate the broadening of our understanding of patterns and processes of evolution as they relate to modularity.

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Modularity and Chunking

The concept of modularity has been used with different meanings in psychology. Among other things, it refers to modular brain structures, to modular mechanisms, and to modular knowledge structures. In this paper, I will focus upon knowledge structures, and discuss the extent to which various knowledge representations can be seen as modular. As a specific example, I will describe the CHREST [Chunk Hierarchy and REtrieval STructures] cognitive architecture, which has been used to simulate data from research into expertise, language, and development. CHREST stores information as nodes in a discrimination network, and uses chunking as its main learning mechanism. In the discussion, I will address how symbolic information-processing systems meet the assumptions of modularity and near-decomposability.

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Modularity in Art

The history of ornamental art began in the period of the middle and late Paleolithic (20-10th millennium B.C.), where we find the first examples of different symmetry structures (rosettes, friezes and ornaments). From the ornamental art of the Neolithic and the first ancient civilizations originate examples of all 17 symmetry groups of ornaments. From the Neolithic date are also the oldest

examples of antisymmetry ("black-white") and colored symmetry groups.
As a modularity will be considered the use of several basic elements (modules) for constructing a large collection of different possible (modular) structures. In science, the modularity principle is represented by a search for basic elements (e.g., elementary particles, prototiles for different geometric structures...). In art, different modules (e.g., bricks in architecture or in ornamental brickwork...) occur as the basis of modular structures. In various fields of (discrete) mathematics, the important problem is the recognition of some set of basic elements, construction rules and an (exhaustive) derivation of different generated structures.

In a general sense, the modularity principle is a manifestation of the universal principle of economy in nature: the possibility for diversity and variability of structures, resulting from some (finite and very restricted) set of basic elements by their recombination. In all such cases, the most important step is the first choice (recognition or discovery) of the basic elements. This could be shown by examples from ornamental art, where some elements originating from Paleolithic or Neolithic art are preserved until now, as a kind of "ornamental archetypes".

As the examples of modular structures lying on the border between the art and mathematics will be considered:

a) antisymmetry ornaments and their derivation from few prototiles, as well as the algorithmic approach to their generation;

b) different knot projections occurring in knot-designs (Islamic, Celtic...), derived from the regular and uniform plane tessellations by using few basic elements.

The main subject of the proposed theme are modular ornamental structures occurring in the prehistoric, their full description, classification and comparative analysis. We will try to show that many ornaments were obtained as the result of the similar or the same work technology (e.g., textile production), derived as modular structures and after that transferred to the other media (bone, stone, ceramics).

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Decomposability and Modularity of Economic Interactions

Although never does the term "modularity" show up in economic textbooks, economic theory is built around a very strong idea of modularity: the entire economic life, as argued by orthodoxy, can be successfully managed by a system in which all information is encapsulated within individual "atomic" economic agents (individual consumers, individual workers, individual entrepreneurs) and coordination is entirely carried out within markets, whereby the only conveyed information concerns the relative scarcity of goods as reflected in prices. This view is epitomised by the so-called "Coase theorem" which states that, even in the presence of interdependencies, coordination can be successfully achieved – at least in principle - via market mechanisms, provided that the granularity of the system is fine enough to encompass all "atomic" economic entities and a proper market exists for each of them (for instance a good is not necessarily the right "grain" and we might need to split it into a multiplicity of independently negotiable rights).

Nevertheless the view of economic systems as organised around a minimal level of granularity is clearly confuted by a straightforward observation of the existence and importance of economic entities – such as business firms – whose grain is much coarser than the one prescribed by a theory which praises the virtues of decentralisation.

Even at a first glance, the aforementioned keywords revolve around some notion of “granularity” of the economic world: e.g., why do we have thousands of different firms rather than a unique and huge one? why are there firms producing cars rather than people buying wheels, windshields, carburettors and assembling them? or, even more radically, people buying raw iron and building cars from scratch? And how new markets get created? That is: how come that economic life is settled at the present level of granularity and aggregation?

We will propose and defend two theses. First, we will claim that the historical evolution of economic systems has created new entities and has settled upon a specific level of aggregation due to integration and disintegration processes and thus that these are the fundamental engine and cause of the world having settled at its actual grain. Secondly, we will ask what would happen if the “economic tape were run twice": will we see again a multitude of firms, producers, consumers, markets and institutions or rather we should see something different? That is: has a god fixed a ultimate and necessary level of granularity of the world or is any level of aggregation possible and attainable?

In this respect, we will present a model of problem solving in which problems are inherently characterised by the presence of interdependencies. We then proceed to a definition of "complexity" of a problem in terms of its decomposability into smaller sub-problems that can independently solved and show that a decentralised market mechanism optimally works as a coordination mechanism only in those cases in which sub-problems are totally independent from one another. In general, however, a trade-off exists between optimality and decentralisation.

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Parts and Parts-of-Parts

Organisms seem to be organized into structural modules, or "parts," presumably on account of a connection between parts and the ability to perform functions. Here, I offer an argument for why such a connection might be expected, in particular, for why a good correlation is expected between number of part types and number of functions. I then advance a hypothesis which suggests a relationship between number of part types — or more precisely, number of types of parts of parts — and the hierarchical structure of an organism. Finally, I discuss some preliminary evidence from a study of parts in bryozoan colonies that supports the hypothesis. More generally, the point is to show how a notion of parts can be operationalized for empirical studies.

Briefly, the argument is this: I define a part as a system that is highly connected or integrated internally and also isolated to some degree from its surround. I then argue that in order to perform a function, a system requires both internal integration, in order to achieve the coordination required for function, and external isolation, to minimize outside interference with that coordination. Therefore, in the evolution of organisms, natural selection can be expected to have localized functions in parts to some extent. (The argument differs from, but parallels, that developed by Wagner and Altenberg [1996] for the evolution of developmental modules.) Some overlap is possible, i.e., one part may participate in more than one function, but few parts should have many functions overlapping in them. Then, arguably, it follows that the variance in number of functions per part type will be low, and therefore that number of part types will be well correlated with number of functions.

If so, a prediction — framed here as a hypothesis — can be made concerning the relationship between numbers of part types and the emergence of new hierarchical levels, such as the evolution of multicellular individuals from aggregates of free-living cells or of individuated colonies from aggregates of multicellular organisms. The hypothesis is that as a higher-level individual emerges and develops the ability to performs functions (presumably as a result of selection), the number of functional demands on the lower-level organisms — and thus the number of functions of which they are capable — should decline. Given the argument above, the number of part types present within lower-level organisms should decline also. In effect, the suggestion is that the lower-level organisms become transformed into parts in the newly formed whole, and in the process lose many of their own internal parts. That is, they lose what are now "parts of parts."

The hypothesis is testable if the notion of "parts" can be operationalized. I suggest a way to do this using "object parts" as a proxy for all parts, and then show how object parts can be identified in practice using boundaries of various types. Finally, preliminary data from a study of bryozoan colonies seem to show an inverse relationship between the average number of part types within colony members (i.e., the number of types of parts of parts) and the degree to which a colony is individuated.

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The Natural Logic of Communicative Possibilities: Modularity and Presupposition

I have claimed that isolable 'properties' (or capabilities) that are required in the development (or evolution) of a communication system are related to each other in a natural structure of presuppositions. The capabilities themselves have an integrity (or modularity) that does not find its ultimate root in the mind or body of the communicator, but in the natural possibilities that constrain communicative systems, a set of possibilities that is in effect for all possible circumstances of communicative evolution. In modern linguistics there has existed a strong tendency to note that human communication develops in a particular pattern, and then to attribute features of the pattern to innate modules of function. It has been claimed that the genes must preprogram the human organism for language. In fact, I suspect, the modularity of linguistic development and function may be largely a result of natural modularity in the logic of the task that presents itself to an individual or a species that would seek to develop a rich communication system. The modularity of the linguistic phenotype results, according to this reasoning, not directly from innate prespecification, but from the fact that a modular communication system provides the optimal (and in some regards the only) solution to the problem of developing a rich communication system. The organism needs general cognitive and vocal tools with which to seek the solution, but need not be assumed to possess many of the properties of a rich communication system innately.

The opinion expressed here is not the product of strictly theoretical efforts, but is instead an outcome of developmental research and evolutionary speculations based upon the results of the developmental work. What is somewhat unique about this empirical research has been its focus on extremely early childhood, in fact on the first months of infancy. Many modern linguists would deny that anything relevant to language occurs in such early infant vocalizations, but I have argued otherwise in the context of a theory that addresses the infrastructure of potential vocal communication systems. Key components of that infrastructure can be characterized as modular 'properties' of potential vocal systems. One of the most primitive properties (Contextual Freedom) involves the ability to produce vocalizations free from stimulus control. While it may not seem like a very rich linguistic event to produce a grunt when no grunt is required by the physics of movement, or to produce a cry in the absence of pain or distress, yet such events clearly represent advances over the typical vocal acts of non-human mammals. This property (or capability) and 15-20 others that I have discussed in The Emergence of the Speech Capacity represent integral types of function in the vocal domain, types of function that are required in all rich communication systems, and that may yield module-like structures of brain capability or, in the case of advanced properties, module-like infrastructural features of language.

I have speculated that the modularity we see in linguistic function is often the result of adaptation (through natural selection in the case of maturationally specified modules, and through self-organization in the case of development) to the requirements that are presented in the form of a natural logic of communicative properties. A key point here is that these posited properties, if I am correct, are not merely the contrivances of a philosophically oriented psycholinguist, but are instead enduring characteristics of the possibilities that confront a potential language learner or a species that might be headed toward linguistic evolution. It appears that these properties can be 'discovered' because they represent unchanging necessities of the task of language, and thus I propose that the specification of the hierarchical structure of the properties should itself become the focus of considerable effort in the formation of an enriched theory of cognition and its roots. Such a pursuit would be 'infrastructural' in nature, focusing upon ultimate constraints that determine the nature of linguistic (and other communicative) behavior.

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Evolutionary Psychology and the Argument from Constraints

"H.A. Simon (1962) considered complexity, or complex systems, to be made up of a large number of parts that interact, or, as the dictionary says, that are connected together... It seems to me the most interesting thing is that parts are often not only numerous, but frequently they are different in their structure and function. ... [U]sually this aspect of complexity gives a division of labor" (Bonner, 1988). The division of labor Bonner is pointing out here occurs in a variety of forms. Wagner and Altenberg argue convincingly that evolutionary adaptation requires the pleiotropic interactions of genes to be local rather than global. Thus, genes form units, or modules that operate in concert to produce some adaptive function. There is also a growing body of evidence for developmental modularity – essentially discrete, localized sequences of events in the process of development from embryo to adult that unfold more or less autonomously from other similar events (Raff 1996). Given the current context, if we were to consider behavior as a biological kind, it would be appropriate to ask, what are the divisions, and who are the laborers? More specifically, how does our behavior decompose into the activities of various capacities and how does the brain support those capacities?

This paper examines one research program that claims to answer these questions. Evolutionary Psychology claims that the brain is composed of numerous modules or information processing devices, each of which is an adaptation selected to resolve some problem our ancestors faced in the distant past. The first section of this essay reconstructs the main arguments for these adaptive modules. In essence the theory claims that given certain constraints, the only kind of brain that natural selection could have built is a brain composed of modules. The second section of the paper argues that even given the aforementioned constraints, there are alternative design possibilities available to natural selection. That is, natural selection is not forced into producing a brain composed of modules under such conditions, and consequently the Evolutionary Psychology project, as it stands, fails. The final section of the paper argues that Evolutionary Psychology may be salvageable. The strategy of looking at constraints external to natural selection and the effects of such constraints on selective processes has proved informative in the past (for example, Bonner 1988). Evolutionary Psychology simply has not exhausted all the relevant constraints in their arguments for modularity. I conclude by offering a few suggestions on evolutionary constraints that strengthen the argument for modularity of mind.

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Morphological Modularity: An Integrative Approach (see Gunther Eble)

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Amphibian Variations - the Role of Modules in Mosaic Evolution

It has long been known that evolution proceeds in a mosaic fashion, modifying some characters but not others in a certain lineage. However, not all characters can evolve independently from each other. As a consequence there may be evolutionary trends, where several characters tend to act as a "unit of evolution", i.e. they tend to coevolve repeatedly, while being easily dissociated from their context.

Such dissociated coevolution may, for example, involve recurrent events of coordinated loss, shifts in timing (heterochrony) or location (heterotopy), or redeployment in new contexts. Recently, it has been suggested that units of evolution will often correspond to developmental or functional modules, where modules can be characterized as highly integrated parts of an organism or some other process or system, which develop and/or function relatively independent from other parts. Focusing on amphibians, I will show how this hypothesis can be tested combining the comparative method with experimental data on development or function. In a first step, the frequency of evolutionary events exhibiting co-dissociation of some characters from others can be assessed by outgroup comparison assuming an explicit phylogenetic hypothesis. This analysis is aided by a new graphic method (heterochrony-plots) that allows to compare the relative timing of a large number of developmental events between two species. In a second step, it can be analyzed whether the frequency of dissociated coevolution of characters correlates with their degree of developmental and functional modularity as identified in experimental studies.

Amphibians are particularly well suited for such a study for two reasons. First, their development is particularly well studied because they have long served as model organisms for developmental biology. Second, they exhibit a variety of life history modes with sometimes dramatic differences in development. The ancestral biphasic life history, with freeliving larval and adult stages separated by metamorphosis, has repeatedly been modified, for instance by the loss of the adult (neotenic salamanders) or the larval stage (direct developing salamanders and frogs). Comparative analysis reveals that many characters that belong to relatively contextindependent developmental modules, have in fact been repeatedly co-dissociated during amphibian evolution. These include thyroid-hormone dependent metamorphosis (multiple loss in urodeles), lateral line placodes (multiple losses), and limbs together with their nerve supply (multiple heterochronic shifts). Further examples are provided by comparing craniofacial and neural development as well as early embryonic processes during gastrulation and neurulation.

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The Structure of Complexity in an Evolving World: The Role of Near-Decomposability

Why does complexity in our universe, at virtually all levels, generally take a hierarchical, nearly decomposable form? The first step toward answering this question is to observe that complex systems had to evolve from simpler systems by processes of evolution. This leads to a second question: What is the connection between speed of evolution and near decomposability?

The answer to this second question is still far from complete, and the incomplete answer we have comes in several parts. First, it is easy to show that, if large systems form by the agglomeration of smaller systems, and if the agglomeration process involves chance meetings between components that can form new, more or less stable, systems, then the probability is very high that large systems will consist of many layers, produced by successive meetings of components – and earlier still, of components of those components – and not by a single "reverse big bang," that instantly assembles a massive system from numerous tiny components.

But not all of the large systems we encounter in the world, especially biological organisms, appear to have been assembled by evolution from diverse smaller components. In particular, the formation of multi-celled organisms has been quite different, mostly based on specialization of identical or similar units that are generated by cell division, but retain a lifetime's mutual attachment. Yet, the same near decomposability architecture appears in these organisms, with their division into organs and tissues, and finally into (specialized) cells. What kind of evolutionary process could lead to the ubiquity of this particular hierarchical scheme?

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Hierarchical Integration of Modular Structures in the Evolution of Animal Skeletons

Living organisms grow by the development of hierarchically organized, modular structures that have non-arbitrary dimensions, defined by scaling considerations and the rates of physical processes. Historically, the evolution of new levels of structural complexity may have been triggered either by the appearance of one or more key adaptations, or by the elimination of previously limiting environmental constraints. When such new modes of structural organization emerge, theoretical models predict a rapid, logistic pattern of increase in the variety of forms, up to a limit defined by the set of viable designs that can exist as transformations of the basic module.

In the evolution of the hard-part skeletons of metazoans, five stages are recognized in the development and permutation of skeletal elements: (1) appearance of simple spicules, scales and cones, with little or no direct linkage between them; (2) elaboration of form by the fusion, differentiation, or serial duplication of structures, facilitating active modes of life at increased body size; (3) development of biomechanically advantageous jointed-lever skeletons, initially by proterstomes and significantly later by deuterostomes with internal skeletons; (4) reduction in the disparity of elements within individual skeletons, often with increasingly consistent patterns of symmetry or regular departures from it; (5) reduction in the total numbers of skeletal elements as these become increasingly well integrated, morphologically and physiologically, and are in some cases lost altogether in specialized taxa. Empirical data are consistent with a rapid logistic expansion and subsequent leveling off in the exploitation of basic skeletal design options by Cambrian metazoans. Metabolic processes evolved at lower structural levels, within cells, were essential precursors of developments in which they would be coopted to secrete hard parts. Skeletal elements themselves coevolved with the soft tissues by which they were formed. Subsequently, feedback from physiological processes and behavior that emerged at higher structural levels was more likely to lead to a reduction than a further increase in the number and variety of hard skeletal elements employed. The rate of exploitation of potential designs to form animal skeletons lies at an intermediate point on a spectrum of acceleration in evolution, driven by increasingly efficient harnessing of energy resources, from the gradual diversification of cell types among unicellular organisms during much of the Precambrian to the explosive proliferation of cultural artifacts unleashed by human behaviour.

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Modularity of Cognitive Organization: Why it is So Appealing and Why it May Be Wrong

Three dominating theoretical approaches in contemporary cognitve science are the computer metaphor, connectionism, and the modularity approach of Fodor (1983) and Marr (1978). All three describe some aspects of human cognitive processes but unfortunately they come too short to become general theories of human cognitive architecture. We concentrate ourselves of the conception of modularity of mind and interpret it as a conception of random (or flat) mosaics of partially autonomous mechanisms. There is increasing evidence, however, that in many cases the relationship between cognitive modules is not as symmetrical as it should be in a perfect parallel architecture. Rather elements of gradiental or hierarchical organization of processing are clearly visible, both in psychological data and in results of neurophysiological studies (Craik et al., 1999; Gabrieli et al., 1996; Velichkovsky et al., 1996). Our analysis of the ongoing research in several domains, such as executive functions, perception, memory, and control of eye movements, demonstrates that the idea of a vertical modularity or stratification (Velichkovsky, 1999) of cognitive organization is more suitable to explain actual empirical data. These emerging heterarchical models of human cognition are discussed from the point of view of

evolutionary roots of cognitive abilities as well as of basic dilemmas of activity organization in changing biological and social environements (Goschke, 2000).

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Evolutionary Mechanisms for the Origin of Modularity

In this presentation a number of studies aimed at elucidating the evolutionary origin of modularity will be reviewed. From the comparison of these results it will be argued that it is very difficult to select for modularity directly. Neither selection for evolvability nor selection for a modular distribution of genetic effects leads to a stable modular architecture. The preliminary conclusion from these results is that there are two possibilities for explaining the origin of modularity.
a) There are additional constraints necessary to allow the stabilization of modular architectures. Population genetic models usually allow for any thinkable variation. It will be shown that these models do not seem to allow stable architectures under directional selection.
b) Modularity is a coincidental by product of a variety of evolutionary processes, like evolution of robustness or gene or character duplication.
It seems that the origin of phenotypic modules shares some features with other “origins problems” like the origin of species and of sex. The processes leading to the origin of entities do not fit into a simple unitary explanatory model.

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Integrated Interaction or Darwinian Competition?
Two Alternative Perspectives on the Behavior of Biological Modules

Well-integrated individuals, such as metazoans, often consist of modules (e.g., genes, organelles, cells, or tissues) which themselves exhibit clear behaviors. Such behaviors include cooperation and competition. Modules cooperate when they induce one another during development, engage in cell-signaling, or are co-involved in producing complex phenotypic traits (e.g., Raff 1996; Wagner and Altenberg 1996; Gerhart and Kirschner 1997). Modules compete when they vie for a common pool of limited resources or access to the germ-line (e.g., Buss 1987; Maynard-Smith and Szathmáry 1995). Modular behavior is approached from at least two different perspectives. (1) The integrated modular interaction (IMI) perspective is concerned with mechanisms for modular communication. Some proponents of this perspective are also interested in how such interaction leads to "emergent" behavior at the organism as well as the superorganism level (e.g., Larsen 1992, Gordon 1999). Modular cooperation, in this view, is understood not as an altruistic act that ultimately increases inclusive fitness, but as a mechanistic and developmental process that establishes the integration of the whole. Modular competition is denied; differential reproductive success occurs solely between the higher-level individuals, organism or superorganism, composed of modules. In contrast, (2) The Darwinian modular competition (DMC) perspective investigates the competitive processes between modules. Modular selection (e.g., gene, organelle, cell, or tissue selection) is conceptualized as part of a hierarchy of selective processes occurring within and between organisms. Adherents of this perspective investigate the relation between selection at different levels (e.g., Otto and Orive 1995; Nunney 1999). While supporters of this view accept that modular cooperation is a mechanistic and developmental process, they explain it either as an altruistic competitive strategy, on the part of modules, to maximize their inclusive fitness or as a behavior enforced by control methods subject to higher-level selection.

Modular competition is accepted; it occurs whenever genetic relatedness becomes too low or the higher-level individual fails to control lower-level selfish variant modules.

A comparison of these two perspectives at two different organizational levels, multicellular and social, or superorganismic, will elucidate their differences. With regard to the multicellular level, I will compare investigations on cell-signaling mechanisms and "simple-minded" interacting genes and cells (e.g., Gerhart and Kirshner; Larsen – the IMI view) with studies on cell-lineage competition (e.g., Otto and Orive; Nunney – the DMC approach). Research on social insects, in particular ants, provides a case study at the superorganismic level. Here I will consider the individual ants as modules of the superorganismic colony. While proponents of the IMI perspective have focused on the integrative properties of ant-colonies (e.g., Schneirla 1971; Gordon), adherents of the DMC view have stressed the ubiquity of genetic conflicts often resolved by kin and multi-level selection (e.g., Queller and Strassman 1998; Bourke and Franks 1995). The substantial differences between the two perspectives become clear in investigating these two case studies. A tri-partite distinction of modules into structural, developmental, and functional modules will aid my analysis (Winther 2000). The two perspectives are relevant for systems with modules that exhibit genealogical properties. Thus, these perspectives also apply to investigations in neurophysiology and artificial life, for example. Although a synthesis of the two perspectives, if at all possible, is desirable, a precise articulation of the differences between them is required for such a resolution.
