

# Thermodynamic Cycles, Developmental Systems, and Emergence

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**Abstract:** The problem of evolutionary emergence is particularly well exemplified in theories of the origins of life and of language. To adequately address these evolutionary problems requires not only deploying the full resources of biological science but also developing a general theory of emergent phenomena that treats biological information and natural selection as a derived, not primitive, features. Currently popular approaches that give genetic reductionism and computational analogies primary roles in their description of the essential organization that constitutes life or mind, ignore the role of self-organization and self-reconstitution in epigenetic systems except as mere expressions of adaptive genetic information. The present approach partially inverts this perspective. We show how use of complex systems dynamics, in the context of developmental systems theory, can provide a general account of evolutionary emergence, in which distributed systemic features can serve as the precursor to localized information replication mechanisms and the natural selection processes these can become enmeshed in. Following ideas explored by Weber and Depew (1996; and Weber 1999), we first apply this approach to the problem of the origin of life. In this hypothesis genetic information emerges as an artifactual molecular re-presentation of the distributed process regularities and self-organization of a dissipative thermodynamic system. The evolution of the dependence of the thermodynamic self-organization of cells on the genetic re-presentation of aspects of these processes, and vice versa, arises spontaneously as this informational redundancy masks selection and causes a partial degradation of the autonomy of component processes. These same fundamental principles are also seen in some ways of construing the Baldwin effect and its role in mental evolution. Understood more generally as a between-levels evolutionary dynamic in which higher order regularities influence lower-order component dynamics, this effect can be seen as a critical contributor to emergent transitions in many aspects of evolution. Following Deacon's (1997) argument that the co-evolutionary emergence of brain and language was driven by Baldwinian processes, the present analysis suggests that the emergence of symbolic communication in human evolution greatly amplified this top-down influence so that it became the dominant factor driving the evolution of human cognition. In summary, the Baldwin effect might not be an anomalous variant of natural selection but rather one example of a class of general mechanisms for evolutionary emergence that can be applied across levels from the origins of life to the origins of the human mind.

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## Introduction

A robust, naturalistic account of the embodied mind and its origin requires the full deployment of the best biological information and theories available. Consciousness may represent a phenomenon that is irreducible and will elude complete explanation as averred by some (Chalmers 1996; Horgan 1999); but it may also be that utilizing evolutionary insights and the tools being developed for

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dealing with complexity we can hope to at least gain insight into the emergence and experience of consciousness (see for example Donald 1991; Edelman 1987, 1989, 1992; Tononi and Edelman 1998; Deacon 1997).

Darwin laid the foundation for the program of a naturalistic, non-dualistic account of mind by providing an evolutionary view of how the human mind might have emerged from antecedent non-human precursors under the influence of natural and sexual selection (Darwin, 1871).<sup>3</sup> Darwin's program was embraced by philosophical and psychological theorists such as Chauncy Wright, for example, an evolutionary account for the origin of human self-consciousness (Wright 1873). Such evolutionary theorizing played a crucial role in the growth of the philosophy and psychology being developed by the American pragmatists (Wiener 1949; see also Godfrey-Smith 1996). More recently, however, most theories of cognition have been based upon computational and information-processing devices, and use contemporary literate, educated western adults as the systems to be modeled. Both approaches are largely unconstrained by evolutionary biology, as pointed out by Merlin Donald (Donald 1991). On the one hand, Darwin's view of the mind as an evolutionary adaptation has receded from the view of many cognitive scientists as they have emphasized the discontinuity of human mind from its evolutionary origins (see for example Chomsky 1980). On the other hand, to the extent that evolutionary biologists have concerned themselves with such questions, they have assumed that the emergence of mind and human language would be explained by the extrapolation of the micro-evolutionary processes described by neo-Darwinism without the need for appeals to developmental neurobiology and computational theories of the origins of mind (see for example Cosmides, 1989, Barkow, Cosmides, and Tooby, 1992, Pinker and Bloom, 1990, and Pinker 1994, 1998 ). Another current line of speculation, informed by the evolutionary gene concept, gives a gene's-eye and meme's eye view of how such replicators can give rise to ever more complex interactor/vehicles that serve to increase their survival in the face of natural selection conceived algorithmically (Dawkins 1976, 1982; Dennett 1991, 1995; Blackmore 1999). Indeed, Susan Blackmore speculates that a meme/gene co-evolution was important in the origin of language (Blackmore 1999). In this, she admits that she is following up, in Dawkinsian terms, on the suggestion of Donald. It was Donald who attempted to shift focus to the steps by which the unique cognitive development of the human lineage would have evolved in which the emergence of symbolic reference became the selective pressure to drive the co-evolution of mind and brain (Donald 1991).

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[3] Interestingly, a preliminary attempt to describe mind in terms of brain physiology, although not in evolutionary terms, was published in 1859 by the Edinburgh professor John Laycock (Laycock 1859). From Darwin's correspondence it is clear that he was aware of this work during the time he was preparing his *Descent of Man*. Of course Herbert Spencer's book on psychology from both naturalistic and evolutionary perspectives was published in 1855 (Spencer 1855). However, Spencer's version of evolution was not Darwinian and had little role for selection; even the subsequent revision of 1870 was little informed by Darwin or natural selection (Spencer 1870).

Throughout the last century, some evolutionary theorists of varying approaches have also invoked additional mechanisms to extend the neo-Darwinian model to better account for the evolution of such remarkably complex and intriguingly prescient adaptations. These include a renewed interest in J. M. Baldwin's theory of "organic selection" (Baldwin 1896) and C. H. Waddington's theory of "genetic assimilation" (Waddington 1940). A few recent theorists have suggested that invoking these concepts may help to account for the very rapid evolution of human language and mental powers by either invoking a determinative role for mental phenomena in evolution or positing a co-evolution of brain and language in which emerging linguistic ability produces a feedback loop upon which selection acts (Dennett 1991, 1995; Pinker 1994; Deacon 1997).

Currently popular approaches, such as evolutionary psychology, downplay the vast range of human variance and cultural diversity that must be taken into account in an evolutionary theory of mind. They also tend to ignore the complex levels of causality that intercede between genes, bodies, behaviors and cultures (e.g. ontogenesis and social evolutionary processes). These simplifying assumptions are complemented by another more sweeping one: viewing the mind to be a set of problem-solving modules of independent evolutionary origin, in the form of embodied algorithms specified by genomic design and capable of independent optimization. This latter view harkens back to the atomistic description of traits by Ronald Fisher, a view that was shown by his contemporaries to offer an unrealistic caricature of the biology of real organisms (Dobzhansky 1937; Wright 1986). Pinker, however, extends this atomistic view further still by assuming that these modules behave analogously to genes, showing phenomena of crossing over and recombination. These curious hypotheses are unsubstantiated and seem to reflect a general pattern of misplaced concreteness pervading the argument, and while not critical to the modularity hypothesis in general, they exemplify a theoretical predisposition to ignore all middle levels of the complex processes that contribute to phenotype expression. We cannot help but feel that such use of evolutionary biology results in a view of mind that falls far short of our experience of consciousness as well as that of the promise held out by an evolutionary perspective. We must ask the following questions. To what extent these simplifying assumptions are merely useful operational definitions for rendering a complex phenomenon more analytically and experimentally tractable? Also, to what extent do they so diverge from the actual causal architecture of evolutionary processes in complex organisms that they direct work away from the critical phenomena in need of consideration? Because these atomistic assumptions exclude consideration of systemic emergent effects at all levels of the analysis, there are good reasons to suspect that this approach will inevitably miss the most critical causal processes behind these mental phenomena they purport to explain.

How then should we proceed to develop a more comprehensive theory of the emergence of mind? A starting point is to ask if the received evolutionary theory offers a sufficiently rich and robust set of concepts to account for the possibility that the cognitive capacities in question are emergent phenomena in evolution?

For example, is this a novel kind of innovation in the same sense as was the origin of life itself? Sterelny and Griffiths argue that any theory of evolution must account for adaptation, pattern of life (diversity, disparity and speciation), and development of organisms over their life cycles (Sterelny and Griffiths 1999). To this list, then, we would add emergence of higher-order novel systems from lower-order systems, as is evident in such major evolutionary transitions as the appearance of eukaryotic cells, multicelled plants and animals, and of course animal and human minds.

The modern evolutionary synthesis (neo-Darwinism or genetical Darwinism) reasonably meets the first two of the criteria of Sterelny and Griffiths, however, developmental biology was largely set aside at the time of the development of the synthesis (Mayr and Provine 1980; Gilbert, Opitz and Raff 1996; Weber and Depew 2000). And since then, in Niles Eldredge's language, developmental biology has not been invited back to the "high table" of evolutionary theory (Eldredge 1995). There are many reasons for this. Clearly one reason is that it has been assumed that development merely represents the channel in the "read-out" of the genetic "program." Hence development is unimportant for evolution except when noise in the channel causes errors in the readout, that lead to an altered phenotype that was not so coded in the genotype. We will address this issue below. But first let's take a closer look at the notion of emergence as it applies to evolutionary biology.

### **Emergent Phenomena**

Darwin set aside the issue of emergence, except as he dealt with the appearance of a complex, sophisticated adaptive structure arising from a primitive one. In discussing the evolution of the eye, an exemplar of organs of extreme perfection, he wrote, "How a nerve becomes sensitive to light hardly concerns us more than how life itself originated..." (Darwin 1859, 187). While this was a defensible strategy for Darwin's time, critics unfriendly to Darwinism charge that the Modern Evolutionary Synthesis continues to ignore problems of emergence. Emergent phenomena would include the origin of complex biochemical systems involved in photo-sensitivity, blood clotting, the immune system, as well as life itself (see for example Behe 1997; but also see a response in Weber 1999). Of late Darwinians of various stripes have deployed the information and ideas from biochemistry and molecular genetics to address these problems, including some utilizing the resources of complex systems dynamics (see discussion and references in Depew and Weber 1995; Weber and Depew 1996; Depew and Weber 1998; Weber 1998, 2000).

John Collier has argued that emergent phenomena in hierarchical systems show several characteristics that need to be addressed in any explanatory model (Collier and Muller 1998)). These include recognizing that emergent phenomena have novel properties not contained in their constituent components and obey laws that rely on these novel properties. Emergent phenomena are not identical to their

composition and cannot be analyzed into their parts and relationships without losing sight of some of their defining characteristics. However, although explanations of micro-emergent phenomena cannot be completely couched in terms of their constituents, the laws governing the constituents are explanatorily relevant. A related point is made by Kauffman, whose simulations of a range of dynamical regimes shows that the order that tends to be produced in these systems more often reflect properties of the whole, rather than properties derived from interactional dynamics of its constituents (Kauffman 1993). The influence of such “generic” properties, as Kauffman refers to them, is both the critical differentiating feature of emergent phenomena and a persistent source of misunderstanding and theoretical difficulty.

One persistent problem with accounts invoking emergent phenomena is that the concept is both ambiguous and used in different ways in different contexts. It is often used in explicitly anti-reductionistic criticisms of standard accounts of such phenomena as life and mind, and has come to be a code-word identified with a complex systems theoretic perspective. In this use, the concept of emergence is often applied as a negative concept in so far as it is meant to apply to phenomena where standard reductionistic accounts fail or seem to incompletely explain apparent discontinuities in properties exhibited at different levels of physical scale. Though this is not the place to review philosophical debates about the reality of irreducible emergent phenomena, it is worth at least distinguishing among different senses of emergence that are commonly confused in discussion of evolution and mental phenomena.

The first sense, which can be called “supervenient emergence” refers is often applied to higher-order properties of an aggregate. One commonly used example is the liquidity exhibited by large aggregates of water molecules. Statistical thermodynamics and quantum theory have provided a remarkably complete theory of how the properties of water molecules can produce liquidity in aggregate, but the relationship isn’t symmetric: this higher-order property is not itself applicable to water molecules. This property emerges with ascent in scale out of the regularities of relationships between molecules, and so the reducibility is not identity. Liquidity supervenes on the properties of water molecules, because these lower-order properties are constitutive of the higher-order property, even if water molecules themselves do not exhibit this property. Philosophical discussions of the mind-brain mystery often invoke some version of supervenient emergence to model the presumed relationship between higher-order mental phenomena and the lower-order cellular-molecular processes on which they depend, but the analogy isn’t quite right. At the very least it fails to capture an essential developmental and evolutionary feature of minds—an unpredictability and novelty-generating capacity that is part and parcel of their adaptive function. We need another more complex sense of emergence that distinguishes where the constitutionality is not so clear. This is the case in systems that develop or evolve over time, and generate successively emergent, not just hierarchically emergent phenomena.

Whereas biological scientists now feel comfortable with the notion that life is an emergent property of organic matter that supervenes on the properties of its constituents, they use a more complex sense of emergence when talking about how life arose from non-life in the early history of the earth. The higher-order properties that constitute a living system themselves emerged over time from conditions in which they did not previously exist. So in addition to being superveniently emergent from the interactions of lower-order entities, there is also a higher-second order emergence involved. In other words, evolutionary processes must be described as the successive emergence of new supervenient emergent phenomena: emergent phenomena constituted of other emergent phenomena. This difference is not merely adding levels upon levels as in the case of the way solid-state physics reduce to atomic interactions that reduce to elementary particle interactions.

This higher-order sense of emergence can in fact be seen to analyze into involve two more complex aspects. Although liquidity is an emergent property, it is characterized by a certain predictability so long as lower-order properties are within certain parameters. But there are conditions where this is not the case: specifically under conditions where turbulent behaviors are produced. Under these conditions certain higher-order regularities become unstable, and an unpredictability of higher-order dynamics results. In such "chaotic" systems, this unpredictability derives from the fact that regularities at lower levels have become strongly affected by regularities emerging at higher levels of organization. This hierarchical nonlinearity produces a kind of self-undermining dynamic across levels. While in principle still superveniently emergent in the above sense, chaotic emergent phenomena cannot be given an account that ignores the history of the system and still maintain descriptive adequacy, whereas merely supervenient emergent phenomena can.

There is a further difference, however, between merely chaotic emergent phenomena, like fluid turbulence, and evolving emergent phenomena, as in living organisms. The latter additionally involve some form of memory (for example, as captured in nucleic acids), that are not seen in chaotic systems. The result is that higher-order regularities can additionally exert a cumulative influence over the causal history of the system, as constraints derived from past higher-order states get repeatedly re-entered into the lower-order dynamics leading to future states. This is what makes the evolution of life both chaotically unpredictable in one sense and yet also historically organized, with an unfolding quasi-directionality, in another sense.

Thus, we can identify three subcategories of emergent phenomena that can be arranged into a sort of hierarchy of decreasing complexity: evolutionary emergence which contains chaotic emergence as a limiting case which in turn contains supervenient emergence as a limiting case. Any given example of evolutionary emergence can also be seen to involve supervenient emergence as well, but not vice versa. The insistent critique from a systems' theoretic perspective of both genetic-reductionistic evolutionary theories and

computationalist cognitive theories can in this way be more precisely rephrased: It is not, then, that there are new classes of phenomena which cannot be explained in terms of lower-level component processes — i.e. understood as supervenient on base material processes — but rather that to treat them as *merely* supervenient (i.e. lacking higher-order to lower-order causal architectures) ignores whole classes of causal relationships that are essential to a comprehensive explanation.

One evolutionary concern that cannot be addressed without incorporating some account of these higher-order conceptions of emergence in their most complex form is the origin of life itself. Another is the origin of human mentality and language. These are particularly troublesome transitions from the point of view of standard neo-Darwinian theory because both involve the appearance of whole new classes of evolutionary processes: the origins of natural selection in the former and the origins of supraorganismic selection processes in the latter. We will consider the special problems presented by these evolutionary transitions below. But it is worth noting at the outset that, although these signature events in evolution stand out as particularly troubling cases, they cannot be considered exceptional in their emergent character. Innumerable other evolutionary developments, responsible for the systemic complexity and functional elegance of so many of the “design features” of organisms, embody the same emergent logic, only less strikingly. So the explanatory principles we seek are not merely needed for the special cases.

### The Emergence of Genetic Information and Natural Selection

The question of how life began is needed to be part of any complete evolutionary theory. As Kenneth Schaffner has argued, the project of reducing Mendelian to molecular genetics would require a plausible account of the origin of life to explain the presence of the cellular structures that function to make DNA replication, transcription, and translation to protein possible (Schaffner 1969). This theoretical vacancy is evident, for example, in Dawkins’ invocation of an ur-replicator/interactor at the origin of life. Thus a single molecule is required to implicitly embody at once both the metabolic-adaptive and the informational-replicative functions of a living organism. Moreover, the theory must be deployed in a conceptual framework that assumes *a priori* both the evolutionary gene concept as well as the genic reductionism concept as givens. But a consistent account of the origin of life need not begin with the assumption that the informational storage component (e.g. via nucleic acid sequences) in a living process is primary. Rather, an account of its evolutionary emergence in an interactional context, e.g. within a self-organizing dissipative chemical system involving multiple types of molecular elements, is also conceivable and provides a more complete account of how the informational and energetic aspects of life became so inextricably linked. This is because the emergent character of the informational aspect of a living process is of a higher order than that of its energetic aspect, and so is dependent on it for its functional significance. In other

words, whereas any self-organizational and reconstitutive features of a chemical system are merely superveniently emergent, to the extent that these regularities become additionally correlated with a patterned physical trace (e.g. embodied in one or more of its components) then there is also an independent possibility of “memory” of this regularity. There can now be an accumulation of higher-order influences implicitly embodied in components capable of directly participating in and thus affecting lower-order dynamics. The information storage function, and a susceptibility to genetic selection, are thus seen as emergent, not primary, properties of life. With their appearance a new class of emergent phenomena emerges as well. A system that exhibited merely supervenient emergent phenomena (and perhaps chaotic as well) now can exhibit evolutionary emergent phenomena.

From this perspective the molecules embodying “replicator” functions (e.g. DNA) can be considered “fossils” — i.e. solidified traces left by an earlier set of higher-order superveniently emergent properties of a molecular system (specifically, traces of its self-reconstitutive statistical regularities). Rather than being left behind with the passage of time, these “fossils” continue to stick around and exert some effect on these ongoing processes. Thus, to the extent that we identify the incorporation of this artifactual re-presentational aspect with the emergence of a new class of evolutionary phenomena, Mendelian and molecular genetics may be considered derivative or rather emergent features of life and yet at the same time be considered part of its defining features. This way of recasting the information processing aspect of living processes as emergent can also have implications for useful ways to connect development and genetics within an expanded evolutionary synthesis. Additionally, it provides a new set of conceptual tools for investigating the emergence of even higher-order information processing features of living systems, such as the origin of mind.

Darwinists committed to a non-expanded evolutionary synthesis, in which natural selection is assumed to be the only significant causal and explanatory mechanism of adaptive design quality and in which genic reductionism is considered primary, have at least implicitly recognized the problems posed by evolutionary emergent phenomena. Many are beginning to try to address the general problem of emergence in a way that maintains their primary commitments. For example, Maynard Smith and Szathmari identify eight transformations in the history of life on earth, in which novel organizational principles have emerged (though they hesitate to use the “e” word). Three of these are in some way involved in the process of the emergence of life from non-life, and hence could be regarded as aspects of a single emergence. In addition to four that involve transformations leading from prokaryotes to eukaryotes and to organisms living in complex communities, they include one of special interest to us, the emergence of language and mind (Smith and Szathmari 1995, 1999). These authors assume that replicating molecules constitute the starting point for the emergence of life and that in general selection acts upon entities that are independent replicators/interactors to embed them in larger emergent wholes in which they can



subsequently only replicate. Like Dawkins they assume a scenario for the origin of life that is replicator first (Dawkins 1976, 1989). It is not surprising for both to say that DNA “lives” in cells, which is a position that is astonishing to most biochemists who study DNA replication in the context of cells. Cells alone fit the usual criteria of living entities for which replication is but one component of several, such as the dissipation of matter/energy gradients through metabolism, ability to respond to and to adapt to changing circumstances, and signal transduction and information processing (Emmeche 1998; Whitesides and Ismagligov 1999).

Maynard Smith and Szathmary posit that the biological order observed and the emergence of new levels of biological organization and phenomena are due solely to the power of natural selection, discounting contributions from any kind of self-organization or any other factor (Maynard Smith and Szathmary 1995). Though natural selection must be a critical explanatory element in the assessment of these transitions, there are real questions as to whether natural selection alone is sufficiently robust to account for full range of the emergent phenomena they discuss, without recognizing how higher-order systemic processes constrain and bias the patterns of the variations presented to selection processes.

Because Maynard Smith and Szathmary are committed to the primacy of selection as sole causal and explanatory agent in evolution, as well as to a reductionism predicated upon replicators, if not genes, as the fundamental entities, it is not surprising that they avoid using the term “emergence.” Instead they prefer to use “transformation” or “transition.” But as we have argued above, to countenance emergence does not require a commitment to holism, but it does mean that the call for explanatory reduction needs to be relaxed and/or that a causal pluralism that allows for parity among possible agents be permitted. The process of emergence of a new replicator, whether it be a gene or a meme, is really not addressed by Dawkins, Maynard Smith and Szathmary, or Blackmore. Rather they assume that once a replicator appears, *no matter by what path or how unlikely*, selection will take over and provide the explanation. This is really not any further along than Darwin’s setting aside the question of the origin of a photo-sensitive nerve. So as interesting as these approaches are, it is not clear that they provide any deep insight into the actual crucial events that lead to the emergence of these new forms of biological order, whether life or language.

These major transitions, like the origin of the information representation function of living systems, each involve an emergent transition, in which, as in this initial transition from a merely chemical system to living system, higher order regularities come to constrain and organize the lower level dynamics in novel ways. The real challenge of explaining these transitions is not in describing how they provide new opportunities for adaptation, or why they may have been selectively favored over prior types of organization. Rather the challenge is in explaining how (other than by exceedingly unlikely accident) the higher-order dynamics of the ensembles came to regulate the dynamics of components’

interactions. This is a question of emergence that is antecedent to questions of selection vis a vis these new units of organism function.

In previous papers by Weber and Depew, an alternative account of the emergence of life that draws upon nonequilibrium thermodynamics and nonlinear dynamics, what might be characterized as complex systems dynamics, using notions of both self-organization and selection, and their *interaction*, is presented. Depew and Weber have argued that, rather than using natural selection to explain the origin of life, we should view natural selection as an emergent phenomenon. Natural selection then is seen as arising from the interplay of chemical selection and chemical self-organization (Depew and Weber, 1995; Weber and Depew 1996, 1999; Depew and Weber 1998; Weber 1998, 2000). This view about the origin of life constitutes a critique of the magic molecule conjecture, according to which life began with a fantastically improbable accident in which a nucleic acid molecule forms spontaneously and happens to find itself in conditions that foster its replication and yet also its structural integrity. These statistically fluky RNA molecules it is supposed persisted long enough through their replicated "progeny" to decorate themselves out with some form of cellular life-boat and survival machines that encapsulates these very special conditions and which is itself produced and controlled by this ancestral replicator molecule. In this scenario is also the critical assumption that natural selection is a special case of physical selection for the stable.<sup>4</sup> Similarly, Weber and Depew's view of prebiotic, or what they have called chemical selection, can be understood to constitute a critique of the rather promiscuous, substrate-neutral conceptions of natural selection. These tacitly imagine that natural selection is like an algorithm that can be spontaneously "implemented" in any number of substrate mechanisms and still retain a life-like function, so that "artificial-life" computer algorithms and memetic processes can also be described as evolving (see for example Dennett 1995).

In this complex systems view of Depew and Weber, natural selection, properly so-called, is not primarily an explanatory model, or a universal mechanism or algorithm. It is itself an emergent phenomenon uniquely characteristic of systems in which information retention and variation facilitates, co-ordinates, and regulates autocatalytic cycling within a set of thermodynamical constraints and imperatives. Any theory of natural selection worth its realistic salt must robustly account for the fact that organisms, like the cells that make them up, are in fact informed autocatalytic dissipative structures. It does not follow from this that natural selection is reducible to chemical selection.<sup>5</sup> What follows is that natural

- [4] Dawkins invokes the notion that natural selection is a special case of physical selection of the stable because the only selective advantage that the first primitive replicator would have would be the extra stability contributed by the hydrogen bonding of base pair formation (Dawkins 1989, 12). Interestingly, the same assumption is made, though from very different motives, by Goodwin (Goodwin 1994, 53).
- [5] In the latter, information is not yet reliable enough, or sufficiently internalized, to produce adaptations. It merely facilitates certain energetic processes. Rather, natural selection arises when the very process that facilitates autocatalytic cycling in open systems by enhancing reproductive fidelity spins off, as it inevitably will, forms of variation whose differential retention leads to specifically biological fitness.

selection presupposes, and can under certain circumstances emerge out of the dynamics of systems in which chemical selection (for a description see Depew and Weber 1998), as we have described it, is at work helping to stabilize an autocatalytic thermodynamic process. It also suggests that in hierarchical, evolving systems we might expect that other selective and self-organizational principles will emerge and be differently instantiated at other levels. Such an account of emergence of life can connect with the approach of the developmental systems theorists. For example, this logic can be brought to bear upon the question of the emergence of language and whether there might be novel or emergent mechanisms possible at that level of the symbolic processes in which language is embedded (e.g. Deacon 1997; and below).

### **Thermodynamic Cycles and Developmental Systems Theory**

Developmental Systems Theory (DST) attempts to show one way that developmental biology can be integrated into a Darwinian evolutionary theory (Griffiths and Gray 1994). It must be noted that not all developmental biologists think that it makes sense to subordinate development to Darwinism. Since the heyday of recapitulationist theories of phylogeny there have been repeated efforts to recast development as the organizing principle of a non-Darwinian evolutionary theory. This is an enterprise that has generated a number of modern developmental evolutionary theories that can be characterized as neo-Geoffroyan (for example Salthe 1993; Goodwin 1994; Webster and Goodwin 1996; see an account in Weber and Depew 1995). The integration of developmental biology and evolutionary theory is currently one of the most serious problems of theoretical biology (Gilbert, Opitz, and Raff 1996). Development and its dynamics plays an important role in the approaches of Edelman (1987) and of Deacon (1997). It is thus of great importance for the program of accounting for the emergence of the embodied mind that there be a robust synthesis of developmental and evolutionary theories.

Systems in which natural selection operates are almost exclusively systems that develop (Weber and Depew 1999, 2000). The integration and regulation of energetic cycles is a primary object of natural selection and adapts organisms to environmental cycles, such as day and night, hot and cold, etc. This occurs only in entities that have a life cycle. The information-bearing components of living systems, such as genes and memes, taken as separate entitative units, clearly cannot be said to adapt. But even in the absence of genetically internalized information, autocatalytic dissipative systems show apparent adaptation in the form of self-regulation and homeostatic responses to external perturbation and may exhibit simple developmental trajectories in which the conditions of one state set the stage for the next. Genetic information offers great opportunities for the stabilization and buffering of developmental trajectories. This is especially so in the earliest and most crucial stages of development, where failure to so stabilize and buffer means death. Indeed, a large body of empirical data documents that the early stages of developmental processes tend to be highly canalized (to use

Waddington's phrase) through genetic mechanisms. Later stages (especially for the development of complex traits), however, are more dependent on other inputs or developmental resources, including external ones for their specification (Weng, Bhalla, and Lyengar 1999). Overall, the developmental process appears to be one in which there is a parity of causal factors, of which genes, though very important, are only one of several (Griffiths and Gray 1994; Griffiths and Knight 1998).

According to DST, entities whose origins lie in natural selection, and on which it can work, are entities that develop in a rather strong sense of the term (Griffiths and Gray 1994). Any such entity is said to be a life cycle, in which a range of developmental resources interact in a complex, self-organizing system in a way that does not depend on a central information source to produce species-specific traits. These resources include genetic information, but also other components of chromosomal, cytoplasmic, and metabolic structures, as well as behavioral, environmental, and social factors. On such a view, DNA does not contain a program that is the sole or primary causative agent, but rather it is one of a number of important resources embedded in a very rich context operating over the whole life cycle (Griffiths and Knight 1998). To the extent that the unfolding ontogenetic trajectory of an organism is determined by a distributed array of sources of information, it cannot conceivably be understood as a set of phenotypic read outs from a genetic program. Yet this is just the assumption that gene selectionism requires, according to such writers as Dawkins and Maynard Smith (Dawkins 1989; Maynard Smith and Szathmary 1995, 1999) and is implicit in the new evolutionary psychology (e.g. Pinker 1998). For such a notion necessarily gives an undue causal role to genes among the ensemble of developmental resources (Griffiths, in manuscript). One might well say in consequence of this rejection that DST is an epigenetic rather than a preformationist view of inheritance (Keller 1995). To do so, however, it is necessary to take some definitional distance from the current meaning of epigenesis, which, under the impact of post-Weismannian thinking, refers to all processes in forming the phenotype other than genetic transcription and translation. Instead, one must gesture toward the older, classical meaning of epigenesis. That meaning ultimately derives from Aristotle's *De Generatione Animalium*, which influenced and inspired the first great modern epigeneticist, William Harvey. Like Aristotle, Harvey held that an organism develops from a process in which the proximate cause of each step is the total set of interactions at the immediately preceding state. This starts with the procreative act, moves through the differentiation and articulation of physical and psychological traits, and ends with the initiation of another life-cycle.

Griffiths, Gray, and Moss have fruitfully brought this conception to bear on the units of selection controversy (Griffiths and Gray 1994, 1997; Moss 1992). Natural selection is viewed by them as acting on developmental processes or life cycles. Variation can arise in principle among any of the resources out of which such a life cycle is constructed, and its differential retention will manifest itself as fitness enhancing changes in aspects of the life-cycle itself, such as changes in developmental timing. These changes can initiate the formation and separation of

evolving lineages. Though perhaps too egalitarian in demoting genetic and promoting non-genetic sources of epigenetic trajectories, DST forces us to recognize that genes are not intrinsically informational. Rather genes are seen as deriving their epigenetic power by virtue of their embeddedness in a web of other self-replicating, self-organizing, self-reconstituting processes through which their influences are expressed.

What evidence is there that forms of weakly, transiently heritable variation, capable of playing the role posited for them by DST, and expected by us in any self-organizing system in which small perturbations sometimes can have large and lasting effects, actually exist? Much of the evidence for such mechanisms has been summarized by Jablanka and Lamb in their *Epigenetic Inheritance and Evolution*. (Jablanka and Lamb 1995; see also Jamblanka and Lamb 1998). A more radical vision of evolutionary change is presented by Steele, Lindley and Blanden in their report of their ongoing studies of the mechanisms and evolution of the immune system. They encounter phenomena that they find are not expected or readily explained by the received view of neo-Darwinism. They assume that they must therefor resort to Lamarckian mechanisms to explain their data (Steele, Lindley, and Blandon 1998). By revising Darwinism, rather than taking its terms for granted, DST and a thermodynamically-informed Darwinism seem to cut nicely between forms of epigenetic inheritance, which play an initiatory role in evolutionary change, and postulated anticipatory, goal-oriented processes. The latter seem to us to be empirically improbable and outside the spirit of Darwinism.

Various cellular entities, such as cytoplasmic factors, organizing centers for basal bodies and microtubules, DNA methylation patterns, membranes, organelles, as well as extracellular factors such as the cellular matrix, developmental and environmental signals, and behavior are referred to as epigenetic inheritance systems (EISs) by Jablanka and Lamb. It is significant that many of these reliable extragenomically transmitted aspects of the cellular-organismic machinery exhibit self-organizational features. In many ways, then, this account of the genes' role in epigenesis parallels the account sketched above (and in previous papers by Weber and Depew) concerning the way that thermodynamically self-organizing systems can serve as the antecedent means for perpetuating and maintaining form across time. This form only later gets represented in more concrete and independently manipulable molecular mechanisms. The net effect of EISs is to provide for natural selection a wider range of a sort of heritable variation than that provided by genetic variation alone. Admittedly, such variations might not be taken up by natural selection in systems that do not exhibit strong, nonlinear forms of feedback and autocatalysis within a self-organizing developmental system. But it is precisely in such systems on the thermodynamic and DST accounts that natural selection is at work. Thus, the contribution of epigenesis to natural selection can be far more than just a channel for gene expression, epigenetic "chunking" of processes is the ultimate arbiter of what constitutes a unit of biological information, and so plays a role in constraining and biasing the variety of forms presented to natural selection. This

is particularly relevant for evolutionary processes that involve cross-level relationships, such as Baldwinian processes. But because there is something that might be called proto-replication in these forms of epigenetic inheritance, there is also some space for heritable variants of these systems to be subject to a kind of natural selection as well. Hence the potential relevance of epigenetic variation is increased.

EISs are responsible, among another things, for cell memory, which ensures that during development and differentiation a cell lineage that has become a kidney cell, for example, continues to produce kidney cells upon somatic reproduction, and not some cell of another lineage or a less differentiated cell. Such stabilizing factors are important in the development of complex metazoans. But any biological process, including those selected for stabilizing and regulating, is, by its very nature, subject to a certain degree of random variation. Grist for the mill of selection is therefore provided within a complex cyclical developmental process.

The best documented example of an EIS is DNA methylation, which is one of the mechanisms of chromatin marking, important for cell memory, in which methyl groups are added selectively to the cytosines of DNA. Genic reductionists too often forget that chromosomes are not exclusively made of up of the base sequences of DNA. Other molecular structures, such as various nucleoproteins and chemical modifications of the DNA bases, such as methylation, may function to affect gene expression. The control of the pattern of methylation during development is not well understood. It is clear that such a pattern is preserved during mitotic division through the action of the methyl transferase enzyme. Methylation has been shown to alter the gene expression of tissue-specific genes, stage-specific genes, and silent genes, whereas the expression of genes needed for basic metabolism of any cell is not so controlled. Differences in DNA methylation lead to different chromatin structures, and so can be considered alternative phenotypes of a gene. Kermicle has suggested that these alternative phenotypes of a particular locus be called "epialleles" (Kermicle 1978). Epialleles arise during normal chromatin alterations that occur during somatic differentiation. Even though such a locus will have the identical DNA sequence, there can be a number of epialleles within an individual organism and in populations. This source of epigenetic variability is expressed during development. It has been demonstrated in several cases, moreover, that epigenetic variation can be transmitted to offspring. Flavell and O'Dell found seven epialleles for wheat high-molecular-weight glutinin that were heritable (Flavell and O'Dell 1990). Sano et al. showed that changes of methylation pattern in rice result in heritable phenotypic change in rice that remained stable over multiple generations, even though DNA sequence was unchanged (Sano, Kamada, Youssefian, Katsumi, and Wabiko 1990). Thus variation in methylation patterns can, in principle, be subject to the action of natural selection, and can lead to evolutionary adaptation by means of various mechanisms, of which Waddington's genetic assimilation is one of the most well known. Evidence that such a mechanism might occur in nature has recently been

reported (Cubas, Vincent, and Coen 1999). A variant in natural populations of toadflax (*Linaria vulgaris*), reported over 250 years ago by Linneaus has been shown to be due to methylation of the *Lcyc* gene that is heritable, rather than due to a base change in the gene. Given evidence of this type of “epigenetic” inheritance in a natural population suggests to Cubas, Vincent and Coen that such mechanisms may be more prevalent in evolution than previously supposed.

In general, plants, which have late to non-existent germ-line segregation, seem to have a greater probability of having epigenetic inheritance play a direct role in having epigenetic variation taken up into adaptationist evolution. Epigenetic factors in animals are more likely to affect early development, or germ-cell lineages. Among animals with complex behaviors, however, the irrelevance of epigenetic variation can be compensated for by increased sensitivity to environmental signals and by behavior.

An additional form of non-germline inheritance has been reported by Lindquist who has evidence of a prion-like protein that is inherited during both cell division and mating-pair interaction, behaving as a heritable unit capable of producing new metabolic phenotypes (Lindquist 1997). Expansion of oligopeptide repeats in the yeast protein results in heritable changes in the fidelity of protein synthesis, such as ribosomes reading through stop codons or suppressing nonsense mutations (Liu and Lindquist 1999). Lindquist has found another prion-like protein that functions in developmental signal transduction such that a number of potential developmental pathways that would lead to phenotypic variation are suppressed except in times of environmental stress; this allows the uncovering of cryptic morphological variation for the action of selection (Rutherford and Lindquist 1998). Also, reliable extracellular inheritance has been demonstrated in certain castes of aphids, where a spurt of growth during the life cycle is possible due to a chemical signal from an inherited, symbiotic microorganism (Morgan and Baumann 1994). Current research in biology seems to be finding a rich number of mechanisms that could be considered as part of the repertoire of developmental resources postulated by DST.

The DST approach to evolution, as well as that informed by complex systems dynamics, preserves the core Darwinian commitment to natural selection as acting upon heritable variation to produce adaptations through differential replication. By changing our notion of the entities upon which natural selection acts, and the ontology in which such entities are most perspicuously described, it simply widens the range of what can count as heritable variation and deepens our notions of the action of natural selection (Gayon 1998). It can, in fact, rightly claim to be more faithful to Darwinism than many current theories in view of its traditional organismic focus, which has been abandoned by genic reductionists, and in view of its fidelity to adaptationism, which some pluralists circumscribe.

### **Emergence in Evolutionary Biology**

It appears that in order to account for some of the major transitions in the evolution of life (and especially its origins) we need to pay greater attention to nongenomic contributions to epigenetic processes at all levels. Particularly important are structures and processes that exhibit some degree of self-organizing character, since these will contribute redundant and predictable informative constraints to developmental processes, almost as if they were being actively replicated in the genome. Indeed, the evidence now available suggests that such regularities even if presented to the epigenetic process extrinsically, become actively recruited and incorporated (a point pursued in greater depth below in relation to Baldwinian processes). This dependency of "hard-coded" genomic information on the "soft-coded" information implicit in self-organizing and self-reconstituting molecular-energetic systems, may in fact recapitulate, in a cryptic way, the likely phylogenetic derivation of this mechanism of genetic control over epigenesis, at the origin of life. Such mechanisms may have their ontological precursors in the formal properties implicit in self-organizing thermodynamic molecular systems.

### **The Baldwin Effect**

This view of life is highly organocentric; but it opens up a much wider range of sources of heritable variation, whose fixation is sometimes accomplished without gene frequency changes at all, while at other times it initiates and precedes changes in gene frequencies. Waddington's genetic assimilation is a good example of the latter (Waddington 1940). It was long regarded as an anomaly by classical neo-Darwinism in spite of empirical support and a plausible mechanism (in which an environmental inducer becomes internalized in the process of development through a genetic change, see for example Gilbert 1997, 821-2). However, it fits smoothly into DST precisely in virtue of the reintegration of genetics and development that DST intends.

The Baldwin effect is another example (Baldwin 1896, 1902). The history of this notion is complex and the effect has been redefined a number of times (see the contributions by Depew, this issue, as well as forthcoming papers by P. Godfrey-Smith and S. Downes presented at the Bennington College Conference on the Embodied Mind). Indeed, the idea was not homogeneous in Baldwin's mind as it was reformulated several times by him, especially in response to the rise of genetics (Plotkin 1988). Although used by Dennett and differently by Deacon, both assume that the Baldwin effect is an established phenomenon or at least a plausible mechanism available for explanatory scenarios. However, there remains a question as to whether there exist satisfactory empirical evidence that the Baldwin effect actually occurs in nature at the levels cited as exemplary. Those phenomena mentioned as evidence for the Baldwin effect are either examples of genetic assimilation, or represent weak linkages of behavior and adaptive



evolution, or may even be irrelevant. The Baldwin effect and genetic assimilation are conceptually distinct mechanisms and need to be evaluated separately (Gilbert 1997; Futuyma 1998, Downes, forthcoming). However, those who assert the equivalence of the Baldwin effect and genetic assimilation aver that there are empirical examples for the Baldwin effect (Hardy 1984; Michel and Moore 1995; Kull 1999, and this issue). What unequivocal “empirical” support there is for the Baldwin effect, as distinct from the mechanisms employed by Waddington, comes from computer simulation. Ackley and Littman combined genetic evolution with neural-network learning in an artificial life “experiment” demonstrating that learned adaptive behavior could, with a stability of both problem and adaptive solution, become encoded in the “genes” (Ackley and Littman 1992). The perceived advantage of the role of the interplay of learning and genetics in this simulation is that the Baldwin effect allows the speed of Lamarckian evolution in a situation where such acquisition of an acquired trait is specifically blocked. Hinton and Nowlan in another simulation experiment also conclude that the Baldwin effect could be of selective advantage by speeding up of the rate of evolutionary change (Hinton and Nowlan 1996). Dennett has recently attempted to hijack the concept by making it refer to large changes that can flow from a hard-wired genetic fluke in a single organism thus giving mind a role in directing evolution. However, the Baldwin effect can be construed to refer to behavioral initiatives by an organism. These could have an effect on development of neonates through forms of cultural mimesis that are sustained and directional enough to result in a shift in gene frequencies over time by whatever mechanism that this might occur.<sup>6</sup> The reported learning of species-specific songs by songbirds while still *in ovo* suggests that in at least some cases behavior can have an effect on developmental pathways chosen during the process of the ontogeny of the information needed for the making of an organism (Gottlieb 1997).

In their tendency to identify heritability with transgenerational selection at the genetic level Darwinians such as Mayr and Brandon can underestimate what DST recognizes. Namely that mimesis and other forms of learning can be heritable over many generations at the phenotypic level and that variant behaviors can already have become adaptively established in a population before any shift in gene frequencies that stabilizes such an adaptation has taken hold. If there is a

[6] In our opinion, one of the nicer consequences that attends this shift in perspective is that it appears to undercut the nasty quarrel about adaptations, traits built by natural selection to serve a function, versus exaptations, traits supposedly built by natural selection for one reason, but coopted, like the panda's thumb, into new ones. What undergirds the intuition that the panda's thumb is an exaptation, in spite of its obvious fitness enhancing properties in the panda's life-cycle, is the stricture that an adaptation must arise from changing gene frequencies under the direct pressure of natural selection. Both Gould and Dennett, the principals in this quarrel, assume this. Failure to meet this criterion is precisely what caused Gould to postulate exaptations, while Dennett argues that exaptations are in fact adaptations because they spring from what he calls “cranes,” gene-based initiatives with large innovative consequences. DST, in rejecting the genocentrism that gives rise to this issue, should have no trouble calling the panda's thumb an adaptation. Nor should it have any difficulty admitting that sea otters in Monterey Bay, who have learned to open abalone shells with rocks brought up from the sea floor, or potato-washing monkeys, have acquired an adaptation.

mechanism by which a selectively advantageous behavioral repertoire can become genetically entrained, so much the better.

A case in point has been reported in matrilineal species of whales—species whose members live with female relatives and form new groups when females and their young fission off from larger groups (Whitehead 1998). It has been reported that these species have five times less diversity in their mitochondrial DNA than humpback whales or dolphins, which do not have such a social structure, while nuclear DNA, the presumptive site of standard Darwinian models of evolutionary change, remains unchanged. Whitehead ruled out empirically many possible causes of this phenomenon. He hypothesized that cultural learning over many generations—the imparting of songs, migration strategies, foraging techniques, or baby-sitting tactics—may become adaptive in ways that are evidenced by, but not caused by, a reduction in genetic diversity in mitochondrial DNA, which hitchhikes on these changes. Mitochondrial DNA is passed exclusively through the female line and is not involved in adaptations except for the biochemical functions carried out by mitochondria. Clearly some sort of evolutionary phenomena is occurring here involving the cultural behavior of the population even though there has been no form of genetic assimilation, nor change of nuclear gene frequencies. From the DST perspective, it is reasonable that such behavior could represent a resource in the life cycle of the whales upon which selection might act, even though it is not clear if some sort of Baldwin effect is at play here.

Whether such specific biological examples as these fit the definition of the Baldwin effect as historically construed or reconstructed, there is a more general question if the more abstract features of the Baldwin effect connect to the general dynamics of emerging evolutionary systems. Having developed an argument about emergence of life and connecting this to the resources of developmental systems theory, we can tentatively explore how the co-evolutionary emergence of human mind and language might reflect similar dynamical patterns of emergence. This may be the level at which the complexity is such that the importance of symbolic re-presentation becomes more dominant and thus more clearly reflects the type of phenomena about which Baldwin was concerned.

### **Steps Toward a Theory of the Emergence of the Embodied Mind**

It seems at least intuitively reasonable, and by weak induction plausible, to expect that if natural selection indeed emerged from chemical selection and self-organization, that there could be a recurrence of such dynamics to produce selective and self-organizational principles at even more complex hierarchical levels.

A possible candidate for such an emergent selection could be Edelman's neuronal group selection given the use made by Deacon and by Edelman of this principle in their account of the origin of language and consciousness (Edelman 1987, 1989, 1992; Deacon 1997; Tononi and Edelman 1998). Edelman has been careful to distinguish neuronal group selection from natural selection even as he

uses it in an analogous fashion. Edelman himself does not consider whether or not neuronal group selection might be an emergent form of selection.

The complexity of even simple nervous systems is vastly greater than that of cells or organs or anything else encountered in nature that it would not be surprising if new dynamical principles would occur in the development of brains (Koch and Laurent 1999). There is ample evidence of a wide variety of self-organizational phenomena in the dynamics of brain organization and action (Kelso 1995). We might well expect then that the selective and self-organizational principles important not only for brain development but also for brain evolution would involve different and richer notions of what counts as heritable, by what mechanisms adaptive selection occurs, and what the units of selection are. Edelman explicitly accepts that the brain is a self-organizing system (Edelman 1992). The spatial/temporal constraints on axonal development, the role of chemical gradients and helper and target cells with their essential supply of nerve growth factor, introduce one new type of self-organizational and selective principles (Edelman 1987, 1989, 1992). These processes produce the primary repertoire of organized neurons, with cells not making connections and getting nerve growth factor dying; the diversity of the patterns suggest an attractor on the chaos side of Kauffman's edge of chaos. It should be noted however, that although Edelman's formulation could well be framed in the discourse of complex systems dynamics, he has not chosen to employ such concepts explicitly. The processes that give rise to Edelman's secondary repertoire involve a different kind of selection in which synaptic connections are strengthened or weakened by biochemical processes reflecting synaptic activity or disuse. The resulting loss of synapses and cells gives rise to functional circuits. The primary and secondary repertoires produce maps of massively parallel and reciprocal connections. By the process of reentry, brain areas emerge that yield new functions. What ultimately is selected are neuronal groups. As groups of neurons are selected, others in reentrantly connected but different maps may also be selected at the same time.

Both Edelman and Pinker assume that there will be an expansion of brain capacity that allows an adaptation for language to emerge, that is brain evolution precedes language acquisition and evolution (Edelman 1992; Pinker 1994). In contrast, Deacon envisions a co-evolutionary emergence of both language and the brain capacity for language (Deacon 1997). Deacon describes this process in the dynamical language of Edelman in which the process of neuronal group selection, developmental self-organization, and a Baldwin-type effect acts through reentry to not only assist development but provide a selection pressure operating at this level.

From both the perspective advocated by Edelman, and that of DST and complex systems dynamics, it is not surprising that a type of selection is acting upon self-organizing developmental resources and diversity during brain evolution. We think that it would be worth a detailed exploration if a similar account of the emergence of neuronal group selection to that of the emergence of natural selection could be articulated. This is a project for another day.

It is possible that novel mechanisms revealed by such analysis might include experiential mechanisms of the sort conceived by Baldwin. It would seem that use of the full resources offered by all these approaches provides the appropriate context for the speculations about the emergence of language and the co-evolution of language and brain structure/function. Peter Godfrey-Smith argues that Deacon's use of the Baldwin effect is in fact a novel extension of the notion to one of niche construction in social ecology (Godfrey-Smith, forthcoming, paper presented at the Bennington College Conference). Godfrey-Smith has noted one of the important features, niche construction, but does not consider how this figures in a broader range of processes that include stress-unmasking and masked distribution.

It may be that the way in which we conceive the Baldwin effect reflects the special emergent complexity in that lineage of primate brains that led to human minds capable of symbolic language. In this sense it is possible that there might not be good instances of the Baldwin effect so construed from phenomena at other levels, since it may be that it can only occur at this emergent level. However, if the principles of emergence as argued above are correct, then the Baldwin effect itself reflects the dynamics of emergent systems more generally, even if its special properties are cryptic in lower-level emergences. The emergence of artifactual genetic re-presentation of distributed systemic process regularities and self-organization during the origin of life, for example, parallels the three modes of Baldwin-like (top-down) processes. These elements, stress-unmasking, niche construction, masked distribution indeed may be essential features of evolutionary emergence of new levels of phenotypic wholes generally. We suspect that these dynamics cover most, if not all, of the major evolutionary transitions discussed by Maynard Smith and Szathmary. These dynamics may be more explicitly visible and more clearly fall within the rubric of Baldwinian evolution in the emergence of human language and mind. This could be due to symbolic communication and language in particular having so vastly amplified the top-down aspect of the dynamic that it has come to dominate natural selection processes in a way not seen in other prior evolutionary processes.

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