A morphogenetic basis for macroevolution?[1,2]

Leigh M. Van Valen
Department of Ecology and Evolution
University of Chicago
915 E. 57 St.
Chicago, Ill. 60637

Received 17 July 1989

There lives in the land of evolutionary biology an approach which is called internalist. Thomson seems sometimes to think that he belongs there, but he doesn't. And it's good that he doesn't, because the internalist approach is either scientifically bankrupt in an obvious way (which Thomson mentions in passing) or merely incoherent. It claims that evolution is to an appreciable extent directed by developmental processes. This either ignores the transition from individual to population, tries to create adaptation by drift or mutation pressure, or uses natural selection while saying it doesn't; different advocates do different things here, but all are equally silly.

The prevailing viewpoint, externalist in this dichotomy, does indeed tend to overlook major aspects of evolution, of which development remains a prime example. By focusing on genetics the standard externalist view overlooks developmental thresholds, lumps the intricacies of development as mere historical constraints, and commonly ignores the necessity of internal coadaptation and the selection required to produce it. Such a theoretical vacuum invites filling, but some fillings are like holograms, having structure but no substance.

The book is narrower in scope than its title suggests. It deals only with animals, especially vertebrates, and especially with the skeleton of the limbs and head. No somatogens need apply. It also largely ignores the control of gene expression in order to show how development itself should be taken seriously. From this perspective, with which I agree, heterochrony is a rather minor fillip on a rich construct, despite its predominance in most evolutionary discussions of development. Most of the book deals with inductive cascades (on which the legends for Figures 10 and 11 are interchanged), developmental integration, and the evolutionary consequences of these phenomena. The first half of the book gives a good discussion of these and other phenomena. Thus terminal addition can't be the usual mode of evolution because determination of new or altered structures normally begins well back in development. Some changes, as in the number of carpal bones, are necessarily discrete but can be threshold effects. Developmental complexity can result in an improved ability (not a narrowed ability, as in machines) to deal with random errors, because of relatively general regulatory interactions which exist as both a cause and an outcome of an organism's self-assembly.

An explicit, though selective, ignoring of much of the older literature does give some problems. Thus in his 1892 book Bateson discussed evidence which indicates that homology among individuals is sometimes not present for single elements like teeth but merely for a whole set of elements. A few others have made contributions later; the subject is intriguing but hardly new. Repetitive homology in general is hardly mentioned in Thomson's book, though, which is a shame because

* * * *

[1] Contribution 100, Lothlorien Laboratory of Evolutionary Biology

[2] **Morphogenesis and Evolution.**
Keith Stewart Thomson. 1988 (1 September). Oxford Univ. Press. vii + 154 pp.
Acid-free paper. ISBN 0-19-504912-8. Hardbound. $29.95.

Evolutionary Theory 9: 329-330 (June, 1990).

complex real examples of it can illuminate problems such as pattern formation. Phenotypic plasticity can illuminate other problems discussed, but it too is nearly ignored; the only use of the term is nonstandard.

Development may affect evolution in nontrivial ways. "I suggest therefore that the principle mode of evolutionary change, as demonstrated by the living and fossil record, is not open-ended progression (however slow and gradual) but sets of clusters that we can call 'themes and variations.' 'Theme' means different ways of doing things biologically and variation here means the range of phenotypic expression of organisms based on that theme" (p. 115, spelling unchanged). The phenomenon is undoubtedly real and was explained by Simpson using adaptive zones. Thomson doesn't even mention this competing explanation; instead he explains the pattern by integrated developmental constraints. (It is only fair to note that Simpson ignored development.) Thomson's explanation has a certain plausibility. From a slightly different perspective, a useful adaptive complex provides an internal environment in which other changes are tested; only compatible changes are accepted, and the process increases the cohesion and resistance to major change provided by the original complex. Plausible, but is it true? How difficult is it to change development in significant ways? The relative ease with which patterns of canalization can be shifted by selection should make us a bit wary. Developmentally oriented evolutionary biologists have a surprising tendency to think of phenomena such as canalization and allometry as more or less immutable, but they aren't. They are characters too, and they evolve like other characters. If there are situations where they don't, it would be important to know this.

A shift to another 'theme' will often, in Thomson's model, involve crossing a developmental threshold, perhaps by the accumulation of many individually small changes in a permitted direction. The new theme is supposed to be both adaptive and already integrated developmentally. There are indeed high-level integrative mechanisms in vertebrates, at least, although it has not, I think, been shown that they produce this result. The pattern (the predominance of clusters of species separated from other clusters by gaps) which is being explained, though, is much more general. It occurs even among prokaryotes. Because the high-level integration necessary is unlikely to be so general, while adaptive zones are if they are looked at properly, there seems to be no real reason to believe in the efficacy of the developmental explanation. However, and emphatically, this doesn't mean that it is always false. Much of it <u>is</u> plausible with respect to vertebrate development, and perhaps beyond, though plausibility is the weakest sort of evidence.

One heretical conclusion which Thomson comes to must, I think, be accepted. This is that evolution occurs at all stages of development, often at early stages of programs leading to the adult. His most conclusive argument for this reminded me a bit of Descartes: Early development does often change; therefore it can. The consequences of this conclusion are only beginning to be explored, but they may include, as Thomson believes, morphologically discontinuous evolution of various degrees. At least such evolution can no longer be rationally dismissed as Goldschmidt's folly.

THE MIND'S NEW CLOTHES[1]

Paul T. Andronis
Department of Psychiatry
University of Chicago
Chicago, Illinois 60637

Perhaps it is a mixed blessing that this remarkable book comes a few years after the heady announcement of the so-called "cognitive revolution" (and the almost simultaneous obituary notice for "behaviorism") in psychology. Patterns, thinking, and cognition outlines a theory of cognition, particularly of "judgement," in a manner at once broadly consistent with the discipline now identifying itself as "cognitive science" (rather than as "cognitive psychology"), and with the field called "the experimental analysis of behavior" (grown from the "radical behaviorist" tradition). This is a scholarly, intellectually challenging, and ultimately impressive book which departs in important ways from past generations of cognitive psychological explanation, but also bears an unfortunate family resemblance as well.

Margolis asserts at the outset that pattern-recognition is the fundamental (atom-like) unit from which all other cognitive abilities derive. In the first half of the book, he quickly introduces us to the various kinds of facts this model must take into account, spells out his assumptions, and then painstakingly develops a formal descriptive system which essentially does what he says it must do, although the general reader is likely to find the exposition somewhat tortuous, and scientists outside psychology (or cognitive science) may find it entirely too abstract.

Among the assumptions made, what strike me as perhaps the most interesting, accessible, and sensible, are the following: motor action (presumably glandular function as well), perception (subjective responses to sensory events), and cognition (learning, remembering, recognizing, judging, reasoning, and so on), alike, probably share common evolutionary lineages, so our understanding of each one should provide important clues about the others (the author describes a "ladder" of cognitive evolution, from primitive feedback systems to learning and more advanced forms of cognition); judgement and other forms of reasoning are inherently contextual and do not follow, even in the broadest sense, the kinds of linear algorithms represented by familiar serial-processing computer programs (hence, the author's out-of-hand dismissal of computer simulations as being essentially incapable of providing us with viable models of cognition); and cognitive attributes of human behavior are evolutionarily continuous with those of other nonhuman species, but exceed them to the extent that we humans can usefully describe complex patterns in the world within and around us, most importantly to ourselves, but obviously to each other as well (a presumably unique attribute we call "language," in contrast to other modes of communication between nonhumans).

The exposition moves quickly beyond these assumptions, and is meticulously and logically argued at such length in the text that it can hardly be done justice by any brief synopsis here. In general outline, it presents judgement as a contextual and recursive process of pattern recognition (hence, the term, "P-cognition"), in which the organism experiences its "Umwelt" only as part of an existing cognitive

* * * *

[1]**Patterns, Thinking, and Cognition**: A Theory of Judgement. **Howard Margolis**. 1988. The University of Chicago Press. xii + 332 pp. ISBN 0-226-50528-6. Softbound. $15.95.

Evolutionary Theory 9: 331-336 (June, 1990).

pattern established by previous exposures, and its current responses become integral parts of that pattern in subsequent exposures. Sensitivity to at least some elemental patterns may be innate, having been built into the organism's neural architecture (presumably, like reflexes) by the selective biological outcomes of its ancestors' repeated exposures and behavioral responses to those patterns. Other more complex forms of P-cognitions are built accretively into individuals' repertoires by experience during their own lifetimes, and act as (Kuhnian) paradigms through which individuals who possess them see the world around them, from its minutest details to whichever "big picture" the individuals' dominant cultures currently support most heavily. On a personal (organismal) scale, differential activation ("cuing") and inhibition of competing P-cognitions is presumably governed by neurological mechanisms similar to those subserving motor and sensory systems, in keeping with the assumption of evolutionary continuity among them all.

This model argues for adding yet another hypothetical element to the already well-populated "black box" inside the organism's head, offering an interesting array of both prosaic and unusual illusions of perception and judgement as evidence that not only "logic + interests" but also "cognitions" (in particular, P-cognitions) are necessary for any adequate explanation of judgement, or indeed any of the "lesser" species of cognitions in the evolutionary hierarchy. Herein lies what I think is the (perhaps most unfortunate) family resemblance to cognitive theories of old: the inherent tacit assumption that the organism makes private cognitive responses to the world around it, and that these are somehow formed independently of public behavior (never mind that our communal evidence for the existence of private cognitive events comes in the first place from some form of public "indicator response"). What does it mean to have a cognition? To be sensitive to complex patterns in worldly objects or events? What are some of the specific behaviors real organisms engage in when we say we know they are thinking, or know that they must have recognized this or that pattern? The fact remains, there is still apparently no independent evidence (again, aside from the behaviors we take as indicators of cognition) that any cognitive "structures" actually exist in more than a verbal/metaphorical sense, or in some universe only parallel to the one through which, say, neurobiology approaches behavior.

Even where electrophysiological events are said to correspond to cognitive ones, we still have behavior as a dependent variable, albeit behavior by structural elements of the nervous system or other anatomical attributes of the organism; this, the enterprise of neurobiology, still requires a physical account of the relevant independent variables, and to my understanding yet requires explicit inclusion of the environmental context in which the behaving unit (whether organism, neuron, neural network, or other) functions at the time the cognitive events are said to occur. Sadly, what is to me the most interesting attribute of the present account is also its most downplayed, namely, explicit formal treatment of the environmental context and of the organism's history of relations with such contexts, as the basis for selection and persistence of particular P-cognitions. And although the organism, its neuroarchitecture, and its cognitive structures seem to serve by turns both as the loci of adaptive changes and as the central causal agents for these same changes, one can have the nagging impression throughout that it is the cognitive structures themselves that actively adapt to real-world events or relations, and that the environment is a passive stage on which the well-clothed mind plays out some pompous soliloquy.

This is puzzling, because the author makes passing (yet repeated) references to behavioral outcomes as being functionally important in directing these adaptive changes, unlike the more traditional and mechanistic "information processing" models which have prevailed in cognitive psychology until recently. Nevertheless, like its predecessors, this model emphasizes P-cognitions as antecedent events, and elaborates on historical changes in their structural organization, all at the

expense of a more careful exploration of relations between behavior with respect to these P-cognitions, and potent contingent consequences, which seem to be the inexorable determinants of those cognitive events in the first place. Antecedent P-cognitions are treated simply as "habits of mind" which comprise and constrain (bias) our perceptions or judgements of the world around us (and through which we take its meanings), but this still leaves us to account adequately for the ontogenic sources of those habits and specific biases, or the means by which environmental contexts somehow select them. And this, afterall, seems to come back to the question of exactly how P-cognitions enter into the socio-cultural contingencies governing the behavioral consequences (read here: prestige or acceptance among professional peers, tenure, access to limited resources for research, social or political freedom, and so on) with which individuals must live after adopting one or another opposing paradigm (i.e., acting on a new P-cognition or an older competing one) -- as noted, this point is passed over relatively quickly in favor of talking about "habits of mind" as though they have lives of their own, independent of their consequences. Psychologists have long recognized effects called "overshadowing" and "blocking" in perceptual behavior, akin to the habits of mind Margolis invokes to explain the resistence often encountered when new P-cognitions first arise. In psychophysical research, such effects are readily related to the biasing influence of the consequences attached to one or another perceptual response, so it might only be a matter of time before the consequences of behavior will be similarly recognized as fundamental (rather than incidental) to explanations of bias and dynamic change in P-cognition.

Recent work in cognitive science (see, for examples, Edelman, 1987; Rumelhart & McClelland, 1986; and Sutton & Barto, 1981) has broken with the older cognitive tradition, and apparently has begun to hit pay dirt with computer simulations which are explicitly "selectionist" in the Darwinian sense, and use parallel distributed processing (PDP) rather than the serial algorithmic processing models which Margolis rightly rejects; these newer PDP models do not depend upon preexisting cognitive structures (or structural "rules"), but upon the "in-structive" or organizing effects of iterated contingency relations between actions of the systems modeled and the selective outcomes or consequences of those actions. Here, amusingly, cognitive scientists almost religiously avoid using the words, "behavior" and "reinforcement," even though their use would be wholly appropriate, and would bring the work of cognitive science into direct contact with the well-developed experimental analysis of behavior (EAB). Moreover, these are both areas to which the present theory of judgement might cleave naturally, although there is only passing mention of exciting new work in PDP and nothing about the EAB. Perhaps in later theoretical explorations, Margolis will incorporate these areas into a plausible descriptive system for the ontogeny of P-cognitions.

Along the way, Margolis more explicitly dismisses both cognitive and behavioral approaches which assume that behavior may be treated as being somehow essentially rational (as though following various forms of economic decision rules) and governed by its consequences. Weighing against this position, the argument goes, is ample evidence that judgements made by experimental subjects often depart systematically from predictions of rationality, even under well-defined test conditions established in the laboratory; our everyday experience (and Margolis, as well) provides generous examples of yet more dramatic departures from economically sound reasoning. Similar arguments against the role of rationality in human action have also appeared recently in other contexts (e.g., Frank, 1989; and Gambetta, 1989), so this may well be an idea which itself rationalizes certain social-intellectual conditions whose time has come for other important reasons. Nevertheless, such criticism seems to miss the point: those who assume behavior (or evolution) is somehow rational generally do so only in a descriptive sense, merely as a heuristic for analyzing what contextual variables might actually govern the observed behavior of organisms (or

evolutionary outcomes). This is not the same as saying that the behavior or evolution of organisms actually "follows" explicit economic decision rules. On the other hand, a legitimate criticism of this approach (at least as applied to organic evolution) is that even the descriptive use of economic models as causal explanations rests upon identification a posteriori of the relevant historical variables, whose plausibility we may well be able to establish, but whose real impact we can perhaps never satisfactorily attempt to falsify. What is left unsaid is that the same problem pervades most cognitive explanations of behavior, the present model included.

The second half of the book is a careful and systematic application of the "P-cognition" formal model to the analysis of historical cases, notably the Darwinian discovery, the Copernican revolution and the trial of Galileo, in part as a plausibility proof of the model, and as an attempt to shed light upon how P--cognitions arising from social/cultural conditions of the times may shape milestone events in our intellectual heritage. The argument is extended to illustrate formally what Margolis calls the "cognitive dynamics" (as opposed to "cognitive statics") driving cognitive changes like Kuhn's paradigm shifts. Here, the argument identifies three phases of paradigm shift: an uphill phase, in which discovery itself takes place, perhaps defining an old problem within a radically new framework, but especially recognizing without need of social confirmation that one has hit upon such a new solution; consolidation, wherein the discoverer becomes convinced of the correctness of the novel solution or new perception, with spread or "contagion" of the new idea among neophytes or converts; and the downhill phase, with detailed elaboration of the new paradigm and ironing out its remaining wrinkles (akin to Kuhn's "normal science").

In the Darwinian example, the uphill phase entailed Darwin's own accretive discovery of patterns of similarity and dissimilarity among species in like and different habitats around the world, and of the exquisite "fit" between the aptitudes of species and details of their environments, all of which made natural selection not only plausible but also nearly inescapable as the explanatory mechanism. That Darwin had read Malthus might account for the particular moment in time when he recognized selection as the explanation for the evolutionary patterns he had observed, but the traditional flash of insightful discovery probably occurred only in hindsight when it came time to explain to others how he had come to think of evolution by selection; in real-time, the exact moment when the thought actually occurred to him probably passed without special notice. The consolidation phase involved settling the matters for others, not simply of whether evolution itself had occurred, but that natural selection was the process through which it took place. This distinction is important because, in the P-cognitive view, there were familiar experiences (like the gradual changes people undergo during growth from infancy to adulthood, plants raised from seeds eventually bearing fruit, and other commonplace developmental phenomena) which made much of the public ready to embrace almost immediately the fact of evolution itself, but none to prepare them for Darwin's account of organisms' exquisite adaptation to their environments by natural selection, as an alternative to grand design executed by a master builder with prior plans; significantly, for nonbiologists in general, there were no firmly entrenched "habits of mind" to compete with "evolution," and to impede its popular acceptance. On the other hand, Margolis notes that, for professional biologists, accepting Darwin's theory of evolution meant abandoning the routine and acceptable debate over the immutability of species (which constituted an important part of the "normal science" of contemporary biology), leading in turn to serious difficulties for many working biologists; possibly most important, they would be forced publicly to reverse expert views previously "hardened" by oft repeated arguments against a theory of evolution that was at once highly plausible and easily accessible to nonbiologists, and therefore popularly accepted even before it gained respectability

among the experts. As a result, professional reputations, patronage, and other powerful social outcomes of scientific expertise stood to be lost or devalued in the bargain, hence, biologists had greater difficulty accepting Darwin's theory than did physical scientists or educated lay persons until the issue of species' immutability and its professional implications were either eclipsed by further developments supporting Darwin's views, or a whole generation of working biologists were exposed to the normal science of evolutionary theory without ever having had to earn a living through work on the species problem.

The remainder of the book's historical exploration devotes two chapters to the Copernican discovery (which, in contrast to Darwin's, apparently came to its namesake as a sudden surprising insight), and another chapter providing a novel treatment of the political polarization (and its P-cognitive basis) in Galileo's trial by the Inquisition, and the Pope's actions the case. Overall, the last half of this book is an important and successful venture which will be of particular interest to those scientists curious about the ways in which cognitive explanations derived from considerations of individual psychology can be usefully applied to formal analyses of social and cultural practices. One misgiving I have about this part of the effort is that history has never performed very good experiments from the standpoint of design. Moreover, all our efforts to recapture the relevant variables which may have operated to produce particular historical outcomes are fraught with known dangers inherent in the inevitably biased selection of remaining evidence about those events by successors with vested interests in particular historical accounts -- and human history often has had more soft body-parts than bony ones. Finally, while its actual outcomes might be strictly determined by specific confluent events, the contingent nature of history makes prediction of future sequences nearly impossible. We are left to content ourselves with what amount to plausible postdictions of what might have been, confirmed by finding what we thought we would when we look to evidence from the past; this smacks procedurally of affirming the consequent (although the present theory handles limited experimental cases in the laboratory quite well and so is vulnerable to empirical disconfirmation). With these reservations in mind, the historical analysis comprising the final half of the book is nevertheless impressive and quite possibly right.

In general, Margolis's theory of judgement deliberately accords with cognitive models in the selectionist camp, yet seems to focus more upon the patterns of organization in the actions rather than on the contextual determinants doing the organizing, and may be considered perhaps most useful as a taxonomy of the <u>outcomes</u> of selection, though I think it may be misleading as a guide to studying the processes by which such outcomes occur. The theory admits that behavior by the nervous system (and indeed the whole organism) is governed by evolutionarily important outcomes of being able to respond coherently to sometimes incomplete or incoherent stimulation. It assumes that real structural elements of the organism (corresponding to inferred cognitive structures) evolved specifically because of their sensitivity to complex patterned stimulation, and that their evolution has been conservative and accretive, hence the resemblance among behavioral processes at all levels, from simple feedback loops to learning, P-cognitions, and judgement. Any really novel attributes of the more recently evolved of these processes would need only arise from the new relations they make possible between the organism and its environment (and not, to be sure, through the evolutionarily recent emergence of any metaphysical cognitive processes). To the extent that P-cognitive structures are indeed real physical components of the behaving organism, with the term "cognitive" simply denoting that we cannot observe their physico-chemical operations occur without special instrumentation which we do not yet seem to have in hand, then this theory can serve as an important set of working hypotheses for experimental, neurobiological, and evolutionary analyses of thoughtful (or should we say, "thoughtly") behavior.

Nevertheless, because of its scope, the tight logical detail of its argument (which the reader must follow closely to apprehend), and the collection of disjointed behavioral anomalies it accounts for plausibly, the appeal of this theory may be difficult to escape should tests of its falsifiability require us to do so. It is also amusing that Margolis's P-cognitive theory shares important aspects of its approach to this subject matter with that taken by radical behaviorism, which was declared dead with the birth of the cognitive revolution. What P-cognitive theory seems to do best is to explicate how whole and complex patterns of stimulation can set the occasion for behavior with important individual and social consequences, but at the same time it neglects the central role of selection by behavioral consequences in its schema; what radical behavioral theory (and the PDP approach to cognition) does best is to explicate the governance of behavior by its consequences on particular occasions, but its systematic examination of control over behavior by complex and competing patterns of stimulation has lagged behind. On the one hand, proponents of either approach are unlikely to do much better without seeing and embracing the strengths the other has to offer; but, as in the case of the newly clad Emperor's court followers, there might be too much at stake professionally for cognitive scientists to give any importance to radical behavioral epistemology, or for the current crop of radical behaviorists to look more closely at complex historical relations between occasions on which alternative behaviors occur and are reinforced by their consequences. On the other hand, evolutionary biologists interested in behavior, (a) who are familiar with the evolution of complex suites of characters, with population outcomes of complex environmental contingencies, and with selection by consequences as a creative and organizing force, and (b) who have no stakes in any particular psychological camp, will (c) probably recognize the important patterns here sooner than the experts in psychology. But then, this seems to be just what the present theory of cognition says is likely to happen if it is correct.

References

Edelman, G. M. (1987). Neural Darwinism: the theory of neuronal group selection, NY, Basic Books. 371 pp.

Frank, R. H. (1989). Passions within reason: the strategic role of emotions, NY, Norton, 304 pp.

Gambetta, D. (1989). Trust: making and breaking cooperative relations, NY, Basil Blackwell, 246 pp.

Purves, D. (1988). Body and brain: a trophic theory of neural connections, Cambridge, MA, Harvard University Press. 231 pp.

Rumelhart, D., & J. L. McClelland (Eds.) (1986). Parallel distributed processing: explorations in the microstructure of cognition, Cambridge, MA, MIT Press/Bradford Books.

Sutton, R. S., and Barto, A. G. (1981). Toward a modern theory of adaptive networks: expectation and prediction. Psychological Record, 88(2), 135-170.