

## **Evo-Devo Meets the Mind: Towards a developmental evolutionary psychology**

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*Draft only: dot-point paragraphs are notes for unfinished sections.*

### **1. What is evolutionary developmental biology?**

In his influential introduction to the emerging discipline of evolutionary developmental biology, Brian Hall defines it as the study of "*how* development (proximate causation) impinges on evolution (ultimate causation) and *how* development has itself evolved" (Hall, 1992, 2 author's emphasis). However, to capture the commitments of most who endorse 'evo-devo' as a scientific program it is necessary to add that the two projects Hall identifies are linked and that the first project is assumed to result in something other than a simple endorsement of current neo-Darwinism orthodoxy. Paying more attention to development is meant to make a difference for evolutionary theory and the new, improved version of that theory is meant to allow more adequate explanations of the evolution of development than were possible beforehand. In contrast, Kim Sterelny has recently argued that it is unlikely that evolutionary developmental biology will lead to findings that are inconsistent with contemporary neo-Darwinian orthodoxy (Sterelny, 2000). Whether or not he is correct, responses to his argument have tended to confirm the view that the current interest in evolutionary developmental biology is tied up with the

idea that it has the potential to alter our understanding of the evolutionary process itself (Love, 2001; Roberts, 2001).

A maximally conservative application of evolutionary theory to developmental biology would merely apply traditional neo-Darwinian theory to a new range of explananda - development. The ways in which organisms develop would be explained in the way that adult phenotypes are commonly explained. Populations of variants change over time so as to better fit the environment they occupy (the lock-and-key model of adaptation). These changes occur when genes are selected because their presence or absence causes a difference in some trait (the gene as unit of selection). This kind of evolutionary explanation of development, however, would not be evo-devo as we know it today. Evo-devo is associated with the idea that paying attention to development problematizes both the idea that form is shaped in a one-sided manner by the demands of the environment and the idea that the unit of selection is the individual gene. Evo-devo problematizes the lock-and-key model of adaptation because the developmental biology of organisms is an input to the evolutionary process as well as an output. The particular developmental biology of an evolving lineage of organisms makes some phenotypes relatively accessible and others relatively inaccessible. Development thus affects the range of variation available for selection and partly determines the evolutionary trajectory of the lineage. Evo-devo problematizes the idea that the unit of selection is the individual gene because it describes emergent levels of organization in the developing phenotype. Although characters at these levels of organization are constructed through the interaction of gene products, they retain their identity when they are constructed using different

developmental resources. The selectionist narratives associated with at least some evo-devo work focus on selection for features at these levels rather than for traits uniquely associated with specific genes or other specific ‘atomic’ inputs to development.

The premiss behind this paper is a simple one. If the ideas that make up evo-devo have been so productive in opening up new lines of investigation in morphological evolution, they may be equally productive for psychological evolution. In the following sections I explore how two of the core theoretical concepts in evo-devo research – modularity and homology – apply to psychology. I examine how the ‘mental modules’ at the heart of much current evolutionary psychology relate to the ‘developmental modules’ that play a prominent role in evo-devo. I suggest that homology as an organizing principle for research in evolutionary psychology, has been severely neglected in favor of analogy (adaptive function). I also examine ‘eco-devo’ – the recent call for evolutionary developmental biology to pay more attention to the ecology of development. I argue that this is a prerequisite for any developmental approach to psychology. In discussing the neglect of homology as an organizing principle and the importance of the ecological context of development, I point out that both these themes were prominent in the classical ethological thought codified by Niko Tinbergen and that they were eclipsed in the late 1960s when sociobiology replaced ethology as the main locus of research into psychological evolution. Finally, I tentatively suggest some likely directions of psychological research that is genuinely developmental as well as genuinely evolutionary.

## 2. Developmental modules and mental modules

The fundamental notion of modularity in evolutionary developmental biology is that of a region of strong interaction in an interaction matrix. A metazoan embryo is modularized to the extent that, at some specific stage in development, it consists of a number of spatial regions that are evolving relatively independently of one another. For example, most events of gene transcription in one segment of a developing arthropod have relatively little effect on the immediate future state of other segments when compared to that of the segment in which the transcription occurs. Developmental modules are typically organized hierarchically, so that modules exist on a smaller physical scale within individual, larger scale modules. The individual cell or cell organelle represents the lowest level of this spatial hierarchy. But although they evolve independently of one another, modules are not windowless monads. The increasing differentiation of various parts of the embryo over time owes a great deal to interactions between modules, as classically described in Hans Spemann's concept of 'induction' in which contact between tissue composed of cells of one type and tissue composed of another causes further differentiation of one or both cell types. The importance of such interactions is entirely consistent with the basic picture of modules as regions that interact more strongly with themselves than with one another. The *immediate* effect of one module on the other is small. Its importance comes from the cascade of *subsequent* events that occurs because of causal connections within the module and not - directly - because of causal connections between modules. For example, the activation of a regulatory gene as a consequence of an interaction between modules is a significant event only because of the resultant

developmental cascade that transforms the affected module into a different type of region within the embryo. A classical example occurs in the development of the eye, with the interaction between the incipient retina and what will later, as a result of this interaction, become the lens.

There are important similarities between the treatment of modularity in evo-devo and the way in which neuropsychology and cognitive science individuate cognitive 'systems'. The claim that two functions are performed by separate systems is supported by evidence of 'double disassociation' - the existence of cases in which the performance of each function is impaired whilst the other is performed normally. Evidence that the ability to recognize people by sight is doubly disassociated from the ability to recognize them by voice is evidence that separate cognitive systems perform face recognition and voice recognition, as opposed to both sensory modalities providing data for an integrated assessment of identity. Disassociation evidence from clinical subjects in neuropsychology plays the same role as embryological evidence of what is also called 'disassociation' in developmental biology: if a region of the embryo can develop normally in the absence of another region, then it is not part of the same module.

- However, developmental disassociation need not imply functional disassociation. That is, the neural or cognitive systems that derive from separate developmental modules may not be functionally disassociated. In the first case, the interaction matrix is made up of the causal interactions that represent the dynamics of the developing morphology of the organism - in the case of the mind, the dynamics of

neural development. In the second case, the interaction matrix is made up of causal relations between components in a fixed functional architecture, in the case of the mind a neural or cognitive architecture. Elements of that architecture could, in principle, be strongly causally interconnected but derive from developmental pathways that are not strongly causally connected.

The use of disassociation studies to document the existence of separate cognitive systems provides a bridge between the developmental modules of evo-devo and the mental modules that play such a prominent role in contemporary Evolutionary Psychology. Evolutionary psychologists often introduce the idea of modularity using disassociation evidence from neuropsychology e.g. (Gaulin & McBurney, 2001, 24-6). However, it is unclear that they *require* that mental modules be disassociable from one another.

Evolutionary Psychologists are clear that modules need not be neurally localized (Gaulin & McBurney, 2001, 26), but their views on experimental dissociability are harder to discern. I will try to establish here that the basic rationale underlying the use of modularity concept in evolutionary psychology requires that modules be developmentally dissociable. If this is correct, then it follows that mental modules are also developmental modules.

The modularity concept of Evolutionary Psychology derives from the concept developed in cognitive science of the early 1980s and examined by Jerry Fodor in *The Modularity of Mind* (Fodor, 1983).

- List of properties from Fodor 1983

Prominent amongst the properties of mental modules in Fodor's account are informational encapsulation, possession of proprietary algorithms and domain specificity. A system is informationally encapsulated if there is information unavailable to that system but which is available to the mind for other purposes. For example, emotional evaluation of a stimulus situation ignores much of what the subject explicitly believes about the situation, suggesting that emotional evaluation is informationally encapsulated (Griffiths, 1990). Most Evolutionary psychologists, however, place more emphasis on domain specificity and the possession of proprietary algorithms than on informational encapsulation. A system is domain specific if it only processes information about certain stimuli. It has proprietary algorithms if it treats the same information differently from other cognitive systems. The two notions are closely intertwined in much of the experimental literature on Evolutionary Psychology. Domain specificity is usually demonstrated by showing that information about one class of stimuli is processed differently from information about another class of stimuli - that is, by showing that this information is processed by devices with different proprietary algorithms. Thus, for example, Leda Cosmides and John Tooby showed that how subjects reason when performing the Wason card-sorting task depends on how the task is described. They argued that certain ways of describing the task activated a domain specific device for social cognition (Cosmides & Tooby, 1992). Likewise, David Buss has used evidence that people leap to conclusions more readily about infidelity than about other subjects to argue that there is a domain specific system for judging infidelity (Buss, 2000). Evidence for separate, domain specific cognitive systems could be provided without postulating that the systems have proprietary algorithms, by demonstrating double disassociation

between deficits in performance on tasks in the two domains. But, as in the two cases just described, Evolutionary Psychologists have not tended to collect evidence of disassociation, concentrating instead on evidence of domain specificity and possession of proprietary algorithm, properties that are typically referred to collectively in the Evolutionary Psychology literature as 'functional specialization'. This is because the evolutionary rationale for the existence of domain specific mental modules requires them to have proprietary algorithms. Separate mechanisms for reasoning about separate domains but reasoning about them in the same way would, from the perspective of evolutionary psychology, be merely bizarre. Evolutionary Psychology argues that evolution would favor multiple modules over domain general cognitive mechanisms because each module can be fine-tuned for a specific adaptive problem. From this perspective, separate mechanisms that deal with separate domains but have identical internal workings simply make no sense.

The evolutionary rationale for mental modules, also implies that modules must be developmentally disassociable. Domain specific cognitive mechanisms are superior to domain general cognitive mechanisms because each mechanism can be fine-tuned by natural selection to be good at performing tasks in a single cognitive domain. If a domain general mechanism was fine tuned in this way, it seems overwhelmingly likely that performance in some other domain would be impaired. If Buss is right that men leap to conclusions about infidelity far in advance of the evidence then it is fortunate that they do not use the same algorithms when deciding whether people are picking a fight. But the independent evolutionary fine-tuning of mental modules assumes that those modules are

developmentally dissociable. If mutations affecting one module typically had effects on other modules then there would be no difference, with respect to their ability to be fine tuned to perform tasks in a single domain, between domain specific modules and domain general cognition. A similar argument suggests that mental modules will be functionally disassociated, since if they are functionally entangled, then changes to one are likely to impair performance in the other. So mental modules are expected to be both developmentally and functionally disassociable from one another, but this is a prediction of 'adaptive thinking', not part of the core of what is meant by modularity in Evolutionary Psychology, which seems to be only functional specialization.

### **3. Modules and Adaptive problems**

The evolutionary rationale for modularity rests on the idea that the environment contains a series of separate adaptive problems. Since the best solution to one problem may not be the best solution to another, a suite of specialized mechanisms will be superior to a single, general purpose mechanism. Similar ideas can be found in evolutionary developmental biology. Günther Wagner and others have constructed population-genetic models in which developmental modularity at the level of gene-control networks is the result of selection for the ability to alter one trait of the organism without altering others (Wagner, 1996). Modularity is selected for because it allows the organism to solve problems separately rather than settling for a single, compromise solution. This selection scenario seems to presume that the environment contains a number of discrete problems (although I will suggest below that this is not really so). Elsewhere, Kim Sterelny and I have identified a fundamental difficulty for the idea that mental modules correspond to

separate adaptive problems, a difficulty which we called the 'grain problem' for Evolutionary Psychology (Sterelny & Griffiths, 1999, 328-332). Whether certain features of the environment of evolutionary adaptedness constitute one problem or many problems depends on the structure of the mind as much as the other way around.

'Problems' whose solutions cannot be developmentally dissociated must be solved as a single problem and so are not separate problems from the standpoint of adaptive evolution.

The grain problem is an aspect of a much better known conundrum in selection theory - the co-constructing and co-defining nature of populations and their ecological niches<sup>i</sup>. It is not possible to take a region of spacetime devoid of life and determine what niches it contains for life to evolve into. It contains many overlapping niches and which ones become actual will depend on the biota that evolves to occupy it. Of course, there is a sense in which every possible niche that an evolving biota could forge in an area of space and time 'exists'. This sense becomes still more tenuous, however, once it is recognized that occupied landscapes owe many of their abiotic properties to the activities of the organisms that occupy them. In this tenuous sense there were niches for species requiring high rainfall in the Amazon Basin before the biota that make it a high-rainfall region had evolved. So a region of space and time contains not only all the niches that can be defined using its existing abiotic features, but also all those that could be defined using features induced by the action of all the species that could evolve so as to make a niche in that region! Some eucalypt species can establish and sustain 'islands' of dry sclerophyll forest

in rainforest by facilitating bushfires (Mount, 1964). The existence of this niche is a result of the evolution of the trees that fill it as much as the reverse.

The grain problem for Evolutionary Psychology results from applying the insight that populations and niches coevolve with one another to the question of how many separate adaptive problems the niche contains. In a trivial sense, the niche contains indefinitely many, overlapping problems and which of these problems the organism adapts to depends on the structure of the organism occupying the niche. Take the example of the evolved basic emotion of fear (Ekman, 1972). Cosmides and Tooby have consistently used the danger posed to our ancestors by predators as an example of the sort of recurring ecological problem that would shape a specific emotional adaptation - an emotion module (Cosmides & Tooby, 2000; Tooby & Cosmides, 1990). But the problem could be viewed in a more coarse-grained way, as that of responding to danger, or in a more fine-grained way as that of responding to snakes or to big cats. The empirical evidence suggests that the actual fear response - the output side of fear - is an outcome of very coarse-grained selection, responding in the same way to danger of all kinds. The emotional appraisal mechanism for fear - the input side - seems to have been shaped by a combination of very fine-grained selection (it is primed to respond to crude snake-like gestalts) and selection to cope with environmental variation (very few stimuli elicit fear without relevant experience).

- There are many ways of parsing the environment into separate evolutionary problems. Although humans have a single fear response, many species have several. Like many animals, Golden Sebright chickens, for example, have one for aerial predators and one for terrestrial predators (Marler & Evans, 1997). More

fine-grained systems can be imagined - a bird's unconstrainedly optimal response to snakes would no doubt be different from its unconstrained optimal response to small, mammalian carnivores. Something must determine how finely an organism perceives its adaptive environment. One suggestion would be that grain-size is optimized given functional constraints such as the costs of obtaining and processing information. Another obvious candidate is the capacity of the organism to developmentally disassociate the mechanisms that respond to the separate stimuli.

- An adequate treatment of the grain problem needs to combine the idea that the emergence of separate modules is influenced by the advantages of more fine-grained responses with the recognition that the environment does not contain any determinate number of separate problems. Perhaps the solution is that once an existing psychological phenotype allows the construction of an organism-referent description of the environment, further finer divisions of resulting taxonomic categories become meaningful?
- Brandon has argued that the units of phenotypic evolution are simultaneously developmental modules and meaningful units of ecological interaction. But why should each developmental module correspond to a single ecological problem? The co-constructing relationship between developmental modules and ecological 'problems' is the key to understanding why these two roles coincide on the same evolutionary units. Problems are individuated in terms of developmentally dissociable responses and the advantages of being able to dissociate responses contributes to the evolution of modularity, as Wagner has argued.

- What is to be understood is change in an organism-environment system over time and focus either on developmental modules as responses to the environment or on organism-referent descriptions of the environment are tactical approaches to decomposing this system to make it tractable for study.
- Work on developmental modules has coped well with the co-constructing relationship between modules and evolutionary problems and has turned this relationship into an actual object of evolutionary investigation. This should be the model for work on mental modules, but it has the cost that the modular structure of the mind cannot be inferred from an independently derived taxonomy of problems in the environment of evolutionary adaptedness. Psychological modules will have to be discovered through a reciprocal growth of knowledge based on simultaneous empirical investigation of the mind and ecological/evolutionary modeling.

### **3. Homology and analogy**

Like Darwin, Hall defines evolution as ‘descent with modification’ (Hall, 1992, 10).

There is a difference of emphasis here with at least some contemporary neo-Darwinists. I suspect that Richard Dawkins, for example, if asked to define evolution in such a few words would be happier with the formulation ‘adaptation by natural selection’. This would better express his commitment to what Peter Godfrey Smith has called ‘explanatory adaptationism’ – the view that the overwhelmingly important task in biology is to explain the adaptation of organisms to their local environment (Godfrey-

Smith, 1999). Hall's preferred formulation draws equal attention to the other major phenomenon which evolution explains, which is the comparative morphology. Whilst both tuna and dolphin are adapted as fast-swimming predators, one is built on a teleost and the other on a mammalian plan. These two explanatory projects are, of course, not only compatible, but, as Darwin famously recognized, they are two aspects of one process:

"It is generally acknowledged that all organic beings have been formed on two great laws - Unity of Type and the Conditions of Existence. By unity of type is meant that fundamental agreement in structure, which we see in organic beings of the same class, and which is quite independent of their habits of life. On my theory, unity of type is explained by unity of descent. The expression of conditions of existence, so often insisted upon by the illustrious Cuvier, is fully embraced by the principle of natural selection. For natural selection acts by either now adapting the varying parts of each being to its organic conditions of life; or by having adapted them in long-past periods of time..." (Darwin, 1964 (1859), 206).

In most areas of biology, the interaction of these 'two great laws' is well understood. The application of that understanding is the 'comparative method' (Harvey & Pagel, 1991). The comparative method can be seen as the use of each of the two patterns in the distribution of forms to illuminate the other. In evolutionary psychology, however, perhaps due to the prominence in recent years of explanatory adaptationists like Dawkins as the public face of evolutionary biology, attention is predominantly paid to the effect of

the conditions of existence rather than to the unity of type. Most work in evolutionary psychology focuses on explaining psychological traits as adaptations to the environment of evolutionary adaptiveness, explanations that categorize those traits in terms of their adaptive function (biological analogy). There is relatively little work focused on explaining psychological traits as the result of descent from a common ancestor, and thus as categories of biological homology.

This situation in contemporary evolutionary psychology is in stark contrast to the situation in the 1950s and 1960s when Konrad Lorenz and Niko Tinbergen reintroduced a Darwinian approach to the mind to the English-speaking world (Burckhardt, 1983). In his Nobel Prize acceptance speech in 1973, Lorenz identified the main contribution of ethology as the recognition that behavior as much as morphology could be treated as a topic in comparative biology. His 'good old Darwinian procedures' (Lorenz, 1966: 274) for the evolutionary study of behavior require that behaviors are homologized *before* adaptive explanations of them are advanced. Identifying where a behavior fits into the comparative pattern is a crucial step in evolutionary explanation for at least two reasons. First, it determines character polarity - the precursor state from which the current state evolved. Offering adaptive explanations without knowing character polarity is like setting out to explain the Second World War without knowing if Germany invaded France or vice-versa (O'Hara, 1988). The second reason why classifying by homology is important is because it allows the application of the comparative method. The best positive evidence for an adaptive explanation is a correlation between the postulated ecological cause and the adaptive response it is suppose to cause. The fundamental methodological

principle in measuring such causes is not to count the number of existing species that display the adaptation in association with the ecological factor, but to count the number of independent originations of the trait (homologies) in association with the original factor.

- Although Lorenz talked of behavior he was actually much like a contemporary evolutionary psychologist in treating behavior as a clue to the existence of abstractly characterized mental mechanisms and using selection to explain those mechanisms. Hence his concepts of displacement activity and superstimulus effect. The displacement of mental mechanisms in favor of behavior itself is a product of sociobiology and its dependence on evolutionary game theory. Contemporary EP is still less focused on mechanisms than was classical ethology, using abstract characterizations of mental mechanisms that are actually behavioral e.g. predator detector, adaptive homicide module. This means that Evolutionary psychology produces explanations targeted at psychological traits defined by analogy - shared function - not by homology.
- This emphasis on analogy is shared by philosophy of mind, which has almost universally assumed that if biology explains psychological traits, then the traits it explains are defined by their adaptive function. Recent exceptions include (Griffiths, 1997; Matthen, 1998, 2000).

- Homology as an organizing principle for the study of psychology has enormous potential but has hardly been exploited. There are a number of reasons why psychological traits defined by homology are actually better targets for psychological study than categories defined by analogy:
  - The logical priority of homology. It simply makes no sense to assign an adaptive function (selection history) to traits unless you first homologize them. Traits do reproduce themselves and so do not form lineages except as parts of organisms. So unless classified as a (Darwinian) homologue a trait does not have a selection history. Any category defined by analogy is either also defined by homology or is the union several categories defined by homology ('convergence').
  - Argument from epistemic access. Ascriptions of adaptive function are typically more epistemically demanding than ascriptions of homology because they are more inferential (philosophers of mind have not realized this because they take as unproblematic high-school examples of convergent evolution e.g. Tasmanian 'tigers', 'eyes'). The ability of the anatomical and physiological sciences to empirically recover homologies without knowing about the evolutionary forces that produced them is encouraging for the prospects of empirically discovering mental modules (see section two above).

- Argument from causal depth. Psychology is in the business of uncovering the mechanisms that produce behavior. Classifications of behavior or of abstractly characterized mental mechanisms should be such as to be heuristically valuable for the study of underlying mechanisms. Similarities due to analogy (shared adaptive function) are notoriously ‘shallow’ - the deeper you dig the more things diverge. Similarities due to homology (shared ancestry) are notoriously deep - even when function has been transformed, the deeper you dig the more convergence there is in mechanisms. Hence homology is more suited to the aims of psychology - and still more to those of neuropsychology - than analogy.

#### **4. *Ecological developmental biology meets the mind***

Niko Tinbergen famously proposed that there were four questions that could be asked about any behavioral trait:

1. What is the evolutionary history of the behavior?
2. What is the current use of the behavior in the life of the organism?
3. How does the behavior develop over the life of the organism?
4. What psychological and other mechanisms control the behavior?

The four questions correspond to four explanatory projects in biology. The first, evolutionary, question is answered by phylogeny reconstruction and evolutionary modeling. The second question is an ecological one: it asks how the trait contributes to the organisms’ capacity to occupy its niche. There is a third question for developmental

biology and a fourth for the cluster of anatomical and physiological disciplines, a cluster that includes experimental psychology and cognitive science.

It is well known that classical ethology concentrated heavily on fourth question, and that much of the best-known work in the period 1935-1955 was framed in terms of Lorenz's drive-discharge model of neurological mechanisms (the 'hydraulic model'). This model and its relatives soon proved inadequate (Hinde, 1956) and they were more or less entirely abandoned by Tinbergen and other ethologists working in the UK and USA . However, many ethologists continued to focus much of their research effort on the proximal causes of behavior, the main successes being in endocrinology.

It is perhaps less well known that classical ethology strongly emphasized the third question. The introduction of Lorenz and Tinbergen's ideas to the English-speaking world immediately after WWII was presented as the rediscovery of 'innate' and 'instinctive' behavior, these terms having a specific sense related to Lorenz's neurological theories. Like those theories, Lorenz's distinction between innate and learned behavior was soon discarded as a result of critiques from ethologists like Daniel Lehrmann (Lehrman, 1953) and later ethologists developed an extremely understanding of gene/environment interaction e.g. (Bateson, 1983; Bateson, 1984). Part of this understanding was a thorough recognition of the role of the ecological context of development in explaining development, and of the role played by organisms in shaping the ecological context in which their offspring develop.

- In an important recent paper, Scott Gilbert has argued that evo-devo needs to pay greater attention to the ecological context of development.
- Importance of ecological inheritance in psychological development.
- Shortcomings of the open program concept as a way of conceptualizing these phenomena - critique of Andy Clark.
- Developmental systems theory as a better way of conceptualizing these phenomena.
- The emphasis on contingency and context-dependence in DST and the contrasting emphasis in evo-devo on developmental structure and its role in stabilizing and entrenching fundamental aspects of morphology can be reconciled in a vision with much in common with Gilbert's vision of 'eco-devo'.

## **5. The evolution of mental development**

- Contemporary evolutionary psychology has an almost preformationist vision of the mind. Plasticity in development is represented as a process of choosing from a suite of facultative adaptations on the basis of environmental cues. If that were what cognitive development is like, then we would have a new evolutionary paradox: why did evolution favor such complex and costly features like a mind and an extended period of post-natal development, while making no more use of them than to detect a cues and respond with predetermined solutions to previously solved problems?
- In the human case, we are dealing with the evolution of 1) a massively extended period of development - *childhood*, 2) an extensive organ(s) for the processing of ad hoc information - *cognition*, 3) the ability to form and perform complex social interaction - *sociality*, and 4) the capacity to produce a new kind of environment

- made out of rites, public knowledge and tradition and preserved by new ways of transmission- *culture* (Griffiths & Stotz, 2000; Stotz & Griffiths, In Press).
- In contrast to contemporary evolutionary psychology, the traditional view is that the function of these 4 features is to react to all sorts of adaptive problems on the run without waiting for multi-generational feedback to build another option into the developmental program. Development, cognition, and culture, it is argued, have been adapted for creating novel *adaptive* behavior. But traditionally, this new domain of adaptation has been seen as isolated from explanation by natural selection, as evolutionary psychologists have pointed out in their critique of the 'standard social science model'.
  - Returning to some of the ideas of the developmentally inclined ethologists e.g.(Bateson & Martin, 1999) would make it possible to accept the traditional view of the role of cognition and culture without drawing a sharp line between adaptation by natural selection and adaptation via cognition and culture. The new mechanisms of ontogenetic adaptation can be 'tweaked' and biased in all sorts of ways by adaptive evolution, as in, to choose the simplest example, the phenomenon of 'prepared learning'. Evolution for flexibility can interact with evolution for bias and for stronger forms of canalization in many combinations, and evolutionary explanations of cognitive traits can take equally many forms.
  - There is a contrast between this suggestion and the emphasis on 'direct' adaptive explanations in current evolutionary psychology. Some theorists display a positive

hostility to explanations that rely on situating evolved mechanisms in a complex contemporary environment to explain a contemporary developmental outcome (citations from Buss, Gaulin). As in evolutionary developmental biology, a developmental evolutionary psychology would recognize that an explanation is not less evolutionary for relying on claims about the developmental structure of the organism to explain why an evolutionary episode has had a particular outcome.

### **References (incomplete)**

- Bateson, P. (1983). Genes, environment, & the development of behaviour. In P. Slater & T. Halliday (Eds.), *Genes, Development & Learning*, (pp. 52-81). Oxford: Blackwells.
- Bateson, P. P. G. (1984). Genes, evolution, and learning. In P. Marler & H. S. Terrace (Eds.), *The biology of learning* (pp. 75-88). Berlin: Springer-Verlag.
- Bateson, P. P. G., & Martin, P. (1999). *Design for a Life: How behavior and personality develop*. London: Jonathan Cape.
- Brandon, R. (1990). *Adaptation and Environment*. Princeton: Princeton University Press.
- Brandon, R., & Antonovics, J. (1996). The coevolution of organism and environment. In R. Brandon (Ed.), *Concepts and Methods in Evolutionary Biology* (pp. 161-178). Cambridge: Cambridge University Press.

- Burckhardt, R. W. (1983). The development of an evolutionary ethology. In D. S. Bendall (Ed.), *Evolution: From Molecules to Men* (pp. 429-444). Cambridge: Cambridge University Press.
- Buss, D. M. (2000). *The Dangerous Passion: Why Jealousy is as Essential as Love and Sex*. New York: Simon and Schuster.
- Cosmides, L., & Tooby, J. (1992). Cognitive adaptations for social exchange. In J. H. Barkow & L. Cosmides & J. Tooby (Eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* (pp. 163-228). Oxford, New York: Oxford University Press.
- Cosmides, L., & Tooby, J. (2000). Evolutionary Psychology and the Emotions. In M. Lewis & J. M. Haviland-Jones (Eds.), *Handbook of the Emotions* (2 ed., pp. 91-115). New York and London: Guilford Press.
- Darwin, C. (1964 (1859)). *On The Origin of Species: A Facsimile of the First Edition*. Cambridge, MA: Harvard University Press.
- Ekman, P. (1972). *Emotions in the Human Face*. New York: Pergamon Press.
- Fodor, J. A. (1983). *The Modularity of Mind: An Essay in Faculty Psychology*. Cambridge, Mass: Bradford Books/MIT Press.
- Gaulin, S. J. C., & McBurney, D. H. (2001). *Psychology: An Evolutionary Approach*. Upper Saddle River, NJ: Prentice Hall.
- Godfrey-Smith, P. (1996). *Complexity and the Function of Mind in Nature*. Cambridge: Cambridge University Press.
- Godfrey-Smith, P. (1999). Adaptationism and the power of selection. *Biology and Philosophy*, 14(2), 181-194.

- Griffiths, P. E. (1990). Modularity & the Psychoevolutionary Theory of Emotion. .  
*Biology & Philosophy*, 5, 175-196.
- Griffiths, P. E. (1997). *What Emotions Really Are: The Problem of Psychological Categories*. Chicago: University of Chicago Press.
- Griffiths, P. E., & Gray, R. D. (2001). Darwinism and Developmental Systems. In S. Oyama & P. E. Griffiths & R. D. Gray (Eds.), *Cycles of Contingency: Developmental Systems and Evolution* (pp. 195-218). Cambridge, Mass.: MIT Press.
- Griffiths, P. E., & Stotz, K. (2000). How the Mind Grows: A Developmental Perspective on the Biology of Cognition. *Synthese*, 122(1-2), 29-51.
- Hall, B. K. (1992). *Evolutionary Developmental Biology*. New York: Chapman and Hall.
- Harvey, P. H., & Pagel, M. D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford & NY: Oxford University Press.
- Hinde, R. A. (1956). Ethological Models and the Concept of 'Drive'. *British Journal for the Philosophy of Science*, 6, 321-331.
- Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (1996). The evolutionary consequences of niche-construction: a theoretical investigation using two-locus theory. *Journal of Evolutionary Biology*, 9, 293-316.
- Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (2001). Niche Construction, Ecological Inheritance, and Cycles of Contingency in Evolution. In S. Oyama & P. E. Griffiths & R. D. Gray (Eds.), *Cycles of Contingency: Developmental Systems and Evolution* (pp. 117-126). Cambridge, Mass.: MIT Press.

- Lehrman, D. S. (1953). Critique of Konrad Lorenz's theory of instinctive behavior. *Quarterly Review of Biology*, 28 (4), 337-363.
- Lewontin, R. C. (1982). Organism & environment. In H. Plotkin (Ed.), *Learning, Development, Culture* (pp. 151-170). New York: John Wiley.
- Lewontin, R. C. (1983). Gene, organism & environment, *Evolution: From Molecules to Man* (pp. 273-285).
- Lorenz, K. (1966). Evolution of ritualisation in the biological and cultural spheres. *Philosophical Transactions of the Royal Society of London*, 251, 273-284.
- Love, A. (2001). *Evolutionary Morphology, Innovation, and the Synthesis of Evolutionary and Developmental Biology*. Unpublished manuscript.
- Marler, P., & Evans, C. (1997). Animal sounds and human faces: do they have anything in common? In J. A. Russell & J. M. Fernández-Dols (Eds.), *The Psychology of Facial Expression* (pp. 133-226). Cambridge: Cambridge University Press.
- Matthen, M. (1998). Biological universals and the nature of fear. *Journal of Philosophy*, XVC(3), 105-132.
- Matthen, M. (2000). What is a hand? What is a mind? *Revue Internationale de Philosophie*, 214, 653-672.
- Mount, A. B. (1964). The interdependence of the eucalypts and forest fires in southern Australia. *Australian Forestry*, 28, 166-172.
- Odling-Smee, F. J. (1988). Niche-constructing phenotypes. In H. C. Plotkin (Ed.), *The Role of Behavior in Evolution* (pp. 73-132). Cambridge, Mass.: MIT Press.

- O'Hara, R. J. (1988). Homage to Clio, or towards an historical philosophy for evolutionary biology. *Systematic Zoology*, 37 (2), 142-155.
- Roberts, J. S. (2001). *Evolutionary Developmental Biology*. Unpublished manuscript.
- Sterelny, K. (2000). Development, Evolution, and Adaptation. *Philosophy of Science*, 67((Supplement)), S369-S387.
- Sterelny, K., & Griffiths, P. E. (1999). *Sex and Death: An Introduction to the Philosophy of Biology*. Chicago: University of Chicago Press.
- Stotz, K., & Griffiths, P. E. (In Press). Dancing in the Dark: Evolutionary Psychology and the Problem of Design. In F. Rauscher & S. Scher (Eds.), *Evolutionary Psychology: Alternative Approaches* (pp. xxx-xxx). Dordrecht, Netherlands: Kluwer.
- Tooby, J., & Cosmides, L. (1990). On the Universality of Human Nature and the Uniqueness of the Individual: The Role of Genetics and Adaption. *Journal of Personality*, 58(1)(March 1990), 17-67.
- Wagner, G. P. (1996). Homologues, natural kinds and the evolution of modularity. *American Zoologist*, 36, 36-43.

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<sup>i</sup> Richard Lewontin was an important early advocate of the idea that niches are shaped by populations as much as the reverse (Lewontin, 1982, 1983). A careful philosophical analysis of the notion of the environment in this context has been constructed by Robert Brandon (Brandon, 1990; Brandon & Antonovics, 1996) and discussed by Peter Godfrey Smith (Godfrey-Smith, 1996) and by Sterelny and Griffiths (Sterelny & Griffiths, 1999). An important program of empirical and theoretical research into 'niche-construction' has been pioneered by John Odling Smee and his collaborators (Laland, Odling-Smee, & Feldman, 1996, 2001; Odling-Smee, 1988). A discussion of these issues from the perspective of 'developmental systems theory' can be found in (Griffiths & Gray, 2001).

