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## **Evo-Devo Meets the Mind: Towards a developmental evolutionary psychology<sup>1</sup>**

Paul E. Griffiths,  
Department of History and Philosophy of Science,  
University of Pittsburgh,  
Pittsburgh, PA 15260  
pauleg@pitt.edu

### ***Abstract***

*The emerging discipline of evolutionary developmental biology has opened up many new lines of investigation into morphological evolution. Here I explore how two of the core theoretical concepts in 'evo-devo' – modularity and homology – apply to evolutionary psychology. I distinguish three sorts of module - developmental, functional and mental modules and argue that mental modules need only be 'virtual' functional modules. Evolutionary psychologists have argued that separate mental modules are solutions to separate evolutionary problems. I argue that the structure of developmental modules in an organism helps determine what counts as a separate evolutionary problem for that organism. I suggest that homology as an organizing principle for research in evolutionary psychology, has been severely neglected in favor of analogy (adaptive function). I consider some arguments suggesting that determining homology is less epistemically demanding than determining adaptive function and argue that psychological categories defined by homology are, in fact, more suitable objects of psychological - and particularly neuropsychological - investigation than categories defined by analogy.*

### **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 straightforward endorsement of neo-Darwinian orthodoxy. A maximally conservative evolutionary approach to developmental biology would merely apply

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<sup>1</sup> In preparing this paper I benefited from the comments of an audience at the Pittsburgh-London Workshop in Philosophy of Biology and Neuroscience, September 2001 at Birkbeck College, London, and to subsequent discussion with two members of the audience, Jackie Sullivan and James Bogen.

contemporary neo-Darwinian theory to a new range of explananda, namely, 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<sup>2</sup>.

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 into 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 – modularity and homology – apply to psychology. Section two examines how the ‘mental modules’ at the heart of today’s Evolutionary Psychology<sup>3</sup> relate to the ‘developmental modules’ that play a prominent role in evo-devo. I distinguish three sorts of module - developmental, functional and mental modules. I argue that mental modules need only be ‘virtual’ functional modules. Evolutionary Psychologists have argued that separate mental modules are solutions to separate evolutionary problems. I argue that the structure of developmental modules in an organism helps determine what counts as a separate evolutionary problem for that organism. In section three, I suggest that homology as an organizing principle for research in evolutionary psychology, has been severely neglected in favor of analogy (adaptive function). I consider some arguments suggesting that

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<sup>2</sup> 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). Sterelny takes a broad view of what is orthodox, but it is certainly true that no leading researchers in the field think of their work as inconsistent with fundamental tenets of Darwinism. In this respect, evo-devo differs from some other ‘developmental’ approaches to evolution, such as process structuralism (Ho & Saunders, 1984).

<sup>3</sup> I capitalize Evolutionary Psychology/Psychologists when used as proper names referring to the doctrines of Leda Cosmides, John Tooby (Barkow, Cosmides, & Tooby, 1992).

determining homology is less epistemically demanding than determining adaptive function. I argue more definitively that psychological categories defined by homology are more suitable objects of psychological - and particularly neuropsychological - investigation than categories defined by analogy. The extrapolation of experimental results in these fields to homologues of the experimental system is warranted, but similar extrapolations to analogues are not warranted by current models of evolution.

## **2. Modularity**

### *2.1. Developmental Modules and Functional 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 developing 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 represents one prominent level of this spatial hierarchy. At a lower level than the cell are particular gene control networks, for example, and at a higher level are classic embryological units like limb buds or arthropod segments. 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 the concept of 'induction'. Contact between tissue composed of cells of one type and tissue composed of another causes - induces - further differentiation of one or both cell types. A classical example occurs in the development of the vertebrate eye, with the interaction between the incipient retina and what will later, as a result of this interaction, become the lens. The importance of such interactions between modules 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 rather than because of the direct causal influence of other modules. For example, the activation of a regulatory gene as a consequence of an interaction between modules is a significant not because of the transcribed product per se, but because of the resultant developmental cascade which transforms the affected module.

There are important similarities between the treatment of modularity in evo-devo and the way in which neuropsychology and cognitive science individuate their 'subsystems' or modules. The claim that two functions are performed by separate neural subsystems has traditionally been established by presenting evidence of 'double dissociation' - sets of clinical or experimental cases in which each function is impaired whilst the other is

performed normally<sup>4</sup>. A recent commentary on the continuing dispute between modular and distributed accounts of brain function gives a characteristic example: “Lesions to temporal areas thought to encompass the FFA [fusiform face area] are associated with prosopagnosia [deficits in face recognition]. Conversely, at least one patient with widespread damage to the visual cortex has shown severely impaired object recognition but selectively spared face recognition.... Such behavioral double-dissociations in response to brain damage provide intuitively appealing evidence of distinct neural mechanisms for processing each type of information” (Cohen & Tong, 2001: 2406). Thus, like developmental modules, neural-functional modules are defined using the idea of semi-decomposability (Simon, 1969). A semi-decomposable system can be divided into sub-systems that are connected internally more strongly than they are connected to one another. The two disciplines have been attracted to the idea that their objects of study are semi-decomposable systems for similar reasons. Semi-decomposable systems can evolve more easily, because the effects of mutations are likely to be localized. They are robust when damaged, for the same reason. They are also relatively easy to study, because in such systems functions are structurally localized. Experimental interventions at different loci in the system have characteristically different effects, making the experimental elucidation of structure-function relationships tractable. Methodologically, the use of dissociation evidence in neuropsychology is paralleled by what is also called ‘dissociation’ 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.

Despite these striking similarities, there is an important difference between developmental and neural-functional modules. In development, the system whose dynamic properties are being studied is the matrix of genetic and other developmental resources that is required for the organism to develop. In neuropsychology, the system is the brain – a piece of morphology at some specific stage in development, traditionally an idealized ‘adult’ stage. When dealing with the brain, then, the two sciences treat it very differently. Neuropsychology regards brain activity as the dynamical expression of a more-or-less fixed neural architecture. Neuropsychologists aim to characterize that architecture. Developmental biology, in contrast, regards that neural architecture itself – extended over developmental time - as a dynamical expression of a developmental system. Developmental biologists aim to characterize the properties of that system. Obviously, these two ways of looking at phenotypic structure are not unique to the brain, but exist for any structure whatever. From now on I will contrast developmental and functional modules in general, rather than developmental and neural-functional modules in particular. The fact that these two kinds of module are actually very different needs to be borne in mind when importing results on modularity from one area of science into another. It is entirely possible, for example, that areas of the brain are parts of a single functional module, but derive from several, separate developmental modules. This relationship is entirely unproblematic - some single bones in the skull, for example, correspond to more than one developmental module (Schlosser & Thieffry, 2000: 1043).

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<sup>4</sup> For a brief history and critique, see (Shallice, 1988: 245-253).

The reverse relationship – in which more than one functional module corresponds to a single developmental module - appears at first to be problematic. The two functional modules have to become separate at some stage, and this would presumably involve the emergence of two separate developmental modules. However, if the separation occurs late in development then most of the work of understanding how these functional modules acquire their characteristic form would be done by studying a single, developmental module. It would, therefore, be safest when comparing findings about modularity in development to findings about modularity in adult function to assume that that the two sets of modules may stand in a many-to-many relationship to one another.

## 2.2. Mental Modules

With the notions of a developmental module and a functional module in hand, I turn to the ‘mental modules’ that play such a prominent role in contemporary Evolutionary Psychology. Evolutionary Psychologists often introduce the idea of modularity using dissociation evidence from neuropsychology (e.g. (Gaulin & McBurney, 2001, 24-6). However, a mental module is a very different thing from a neural-functional module. Evolutionary Psychologists themselves are quite clear that their mental modules need not be localized in single regions of the brain (Gaulin & McBurney, 2001, 26). I will argue that they need not be neural-functional modules in any standard sense. In neuropsychology, the double dissociation experiment is a means for exploring structure-function relationships in the brain. But for the purposes of evolution, what matters is not how the brain is structured, but how it appears to be structured when ‘viewed’ by natural selection. For Evolutionary Psychology, the fact that two functions are dissociated is significant in its own right, and not only as a clue to how those functions are instantiated in the brain. Thus, there are architectures that produce double dissociations but which neuropsychology regards as non-modular. Evolutionary Psychology, in contrast, would regard these architectures as different ways to produce mental modularity. We might aptly term such mental modules ‘virtual modules’.

The modularity concept of Evolutionary Psychology derives from that developed in cognitive science of the early 1980s and synthesized by Jerry Fodor in *The Modularity of Mind* (Fodor, 1983). In Fodor’s account, the definitive property of a module is informational encapsulation. 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, in a phobic response the emotional evaluation of a stimulus situation ignores much of what the subject explicitly believes about the situation, suggesting that the emotional evaluation is informationally encapsulated. Fodor lists several other properties of modules, including domain specificity and the possession of proprietary algorithms. 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 subsystems, something that Evolutionary Psychology identifies with the older idea that the module has ‘innate knowledge’. John Tooby and Leda Cosmides

make it clear that it is these two properties, rather than informational encapsulation, that are the two definitive properties of mental modules. A mental mechanism is not a module if "It lacks any a priori knowledge about the recurrent structure of particular situations or problem domains, either in declarative or procedural form, that might guide the system to a solution quickly." (Tooby & Cosmides, 1992: 104). In the Evolutionary Psychology literature the properties of being domain specific and of having proprietary algorithms are generally referred to simultaneously as 'functionally specialization'. Modules are "complex structures that are functionally organised for processing information" (Tooby & Cosmides, 1992: 33).

When Evolutionary Psychologists present experimental evidence of domain specificity in cognition, it is generally evidence suggesting that information about one class of stimuli is processed differently from information about another class of stimuli - that is, evidence of the use of different proprietary algorithms in the two domains. For example, Cosmides and Tooby showed that how subjects reason when performing the Wason card-sorting task depends on how the task is described. They used this to argue that certain ways of describing the task activate a domain specific device for social cognition (Cosmides & Tooby, 1992). Similarly, David Buss has presented evidence that people leap to conclusions about sexual infidelity more readily than about other subjects. He uses this to argue that there is a domain specific system for judging infidelity (Buss, 2000). Evidence for separate, domain specific cognitive systems could, of course, be provided without postulating that the systems have proprietary algorithms. This could be done if the evidence for domain specificity came from dissociation studies. There is no conceptual difficulty in demonstrating double dissociation between deficits in performance on tasks in two domains while simultaneously showing that information about the two domains is processed using the same algorithms. The brain might resemble a computer network with two identical mail servers, one used by the sales department and the other by the accounts department. Both run the same software, but when one goes down it causes a distinctive set of performance deficits! However, Evolutionary Psychologists have not tended to collect evidence of dissociation, relying instead on evidence that the brain has 'innate knowledge' of certain domains, as in the two cases just described. In fact, if dissociation results were available but there was no evidence of 'innate knowledge', Evolutionary Psychologists would not regard these functional modules as mental modules as the quotation from Tooby and Cosmides makes clear. 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 Psychologists argue that evolution would favor multiple mental 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 make no evolutionary sense.

The evolutionary rationale for mental modules also implies that mental modules must be developmentally dissociable. Domain specific modules are superior to domain general cognitive mechanisms, it is argued, because each module can be fine-tuned by natural selection to be good at performing tasks in a single cognitive domain. But independent evolutionary fine-tuning of mental modules requires that those modules are developmentally dissociable. If mutations affecting one mental module typically had effects on other mental 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 dissociated, 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 dissociable 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. In fact, as I suggested above, mental modules might sometimes be only 'virtual modules' from the viewpoint of neuropsychology. A virtual module, recall, is a pattern of dissociability between aspects of the systems performance that does not correspond to the existence of separate neural systems. Tim Shallice describes six kinds of neural architecture that can produce double dissociation without corresponding functional modules (Shallice, 1988: 250). It would take far too long to describe all these here, so I will give only the simplest one. If a range of inputs is processed by a continuum of processing space in the brain, as is the case for inputs across the visual field and areas of visual cortex, then lesions to specific portions of that processing space will affect specific domains of input. It would not be illuminating, however, to divide such a continuous processing space into several discrete modules, or the corresponding input domain into several domains. This admittedly rather trivial example illustrates an important general point. Neuropsychologists use dissociation results to study structure, function and structure-function relationships in the brain. They have become aware in the last fifty years of many difficulties in interpreting dissociation results and have come to treat dissociation as suggestive evidence in need of further interpretation. A modularity concept that simply identified a module with a neural system that produces double dissociations would not be useful for neuropsychology because it would serve only to blur distinctions between different neural architectures. Evolutionary Psychology, in contrast, is interested in what the brain must be like if it is a product of evolution. Central to the research program of Evolutionary Psychology is an argument that selection will favor many, functionally specialized modules rather than a few, domain-general cognitive mechanisms. The argument relies on a 'thin' definition of a module that counts as modular any architecture that produces dissociations between performances in different domains. This is entirely in keeping with the fact, strongly emphasized by many evolutionary psychologists, that they offer a theory of function and not of structure:

When applied to behavior, natural selection theory is more closely allied with the cognitive level of explanation than with any other level of proximate causation. This is because the cognitive level seeks to specify a psychological mechanism's

function, and natural selection theory is a theory of function. (Cosmides & Tooby, 1987: 284)

Since the aims of the two disciplines are so distinct, it is unsurprising that they have different concepts of modularity<sup>5</sup>.

### *2.3 Modularity and Adaptation*

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. I am not concerned to assess the soundness of this argument here, only to explore its consequences. Closely related 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). We suggest that whether certain features of the environment of evolutionary adaptedness constitute one problem or many problems depends on the developmental structure of the mind. 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>6</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

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<sup>5</sup> I believe that the same is true of developmental biology, and that a mental module ‘virtual’ with respect to developmental modularity is possible, but I have not yet developed an adequate defense of this view.

<sup>6</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).

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 can be defined using biotic and abiotic features that could be created 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 regions by facilitating bushfires (Mount, 1964). The existence of this niche in that region of space and time is a result of the evolution of the trees that fill the niche 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. An obvious example is 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 the problem of responding to danger, or in a more fine-grained way as the problem of responding to snakes on the one hand or to big cats on the other. The empirical evidence suggests that in humans the actual fear response - the output side of fear - is an outcome of very coarse-grained selection, since it responds 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, since it is primed to respond to crude snake-like gestalts, and selection for developmental plasticity, since 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 other animals have one fear response for aerial predators and another quite different fear response for terrestrial predators. More fine-grained systems can readily be imagined - a bird's unconstrainedly optimal response to snakes would no doubt be different from its unconstrained optimal response to small, mammalian carnivores. So the idea that the environment itself sets a determinate number of problems that impose a structure on the mind is inadequate. Something must determine how finely an organism perceives its adaptive environment. One suggestion would be that grain-size is optimized given constraints such as the costs of obtaining and processing information. Those costs, of course, will be a function of existing mental structure, amongst other things. Another obvious candidate is the capacity of the organism to developmentally disassociate the mechanisms that respond to the separate stimuli. I do not pretend to have a final solution to this problem and it is in any case clear that empirical research is needed as well as conceptual clarification. However, I suggest

that any adequate treatment of the grain problem will need to combine the idea that the emergence of separate mental modules is influenced by the selective advantages of a more fine-grained response to the environment with the recognition that the environment does not contain any determinate number of separate problems. One way to satisfy these two desiderata would be to postulate a co-evolutionary process in which the psychological phenotype of an organism at some point in time imposes a structure on the environment (for example, dividing it into ‘aerial predation’ and ‘terrestrial predation’) and that intrinsic features of the environment then afford the possibility of sub-dividing that structure (for example, into ‘terrestrial - snake’ and ‘terrestrial - cat or quoll’). A co-evolutionary picture of this kind would be consistent with Robert Brandon’s claim (Brandon, 1999) that the units of phenotypic evolution are simultaneously developmental modules and ecologically meaningful units that correspond to some set of features in the selective environment (*sensu* (Brandon, 1990)). Why should each developmental module correspond to a single ecological problem? The co-constructing relationship between developmental modules and ecological ‘problems’ would tend to ensure that, as a result of evolution rather than as a matter of definition, these two ways of ‘parsing the phenotype’ would coincide on the same units. Ecological problems are individuated in terms of developmentally dissociable responses and the advantages of being able to dissociate responses contributes to the evolution of developmental modularity.

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. The less we know about the human mind, the less we know about the structure of the environment that shaped it. Psychological modules will have to be discovered through a reciprocal growth of knowledge based on simultaneously empirical investigation of the mind and its development and ecological/evolutionary modeling of mental evolution. Work of this kind in evolutionary psychology would resemble contemporary evo-devo research into the evolution of morphology.

### **3. Homology**

#### *3.1 The Unity of Type and the Conditions of Existence*

Like Darwin himself, Brian 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, if asked to define evolution in as few words

as possible might 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 of biology is to explain the adaptation of organisms to their local environment (Godfrey-Smith, 1999, 2000). Hall’s preferred formulation draws equal attention to the other major phenomenon that evolution explains, which is 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, 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, perhaps the single most powerful epistemological technique available to biology (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. Evolutionary Psychology, however, attends predominantly 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’. These explanations categorize psychological traits in terms of their adaptive function (biological analogy). There is relatively little work explaining psychological traits as the result of descent from a common ancestor, and thus explaining them as homologues. This emphasis is perhaps due to the fact that explanatory adaptationists like Dawkins have acted as the public face of evolutionary biology in recent decades.

The 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 psychology 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 behavior be homologized before adaptive explanations 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 American Revolution without knowing if the United States seceded from the United Kingdom 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 supposed 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. Conversely, the easiest way to test adaptive hypotheses is usually to test predictions about the comparative pattern of the homologous traits that figure in those hypotheses<sup>7</sup>.

The emphasis on analogy in contemporary Evolutionary Psychology is shared by contemporary philosophy of psychology. With a very few exceptions (Griffiths, 1997; Matthen, 1998, 2000), philosophers appear unaware of the possibility of classifying behavioral, psychological and neurological states by homology. Philosophers have hotly debated the value of thinking about the mind in terms of adaptive function, but both sides have assumed that if biology does, in fact, offer valuable explanations of psychological traits, then the traits it explains must be defined by their adaptive function. Some work by Valerie Hardcastle shows just how deeply engrained this idea has become. Hardcastle responded to my proposal that emotional states should be classified by homology (Griffiths, 1997) by arguing that this 'evolutionary' classification is unhelpful because it classifies things by the reason that they evolved, that is, by adaptive function! Hardcastle writes: "even if some anatomical structures are homologous across whatever domain interests the scientists, this does not entail that the structures should be thought of as a single kind of thing from the perspective of neuroscience. ... They [scientists] want to know what various structures are doing now in an organism, not what led to their being there over evolutionary time. ... Neurophysiologists and neuropsychologists want to know what roles and responsibilities isolated brain structures have, and not so much why we have them in the first place. Though an evolutionary perspective can certainly be useful in thinking about functions and individuating psychological categories, the buck doesn't stop there." (Hardcastle, 1999: 244). Hardcastle has imbued the idea that evolution = adaptation so thoroughly that she assumes that any 'evolutionary' approach must involve classifying traits by the purpose for which they were designed. Misunderstandings aside, I think Hardcastle's position and my own are actually very close. She is happy to classify brain structures in the traditional way using anatomical categories like 'amygdala' and 'cingulate cortex', which, like all traditional anatomical categories are categories of homology. Conversely, I agree with her that knowing the actual causal role of brain structures is the ultimate goal of neuroscience and that homology is of interest to

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<sup>7</sup> For a methodological overview of the use of the comparative method in the study of adaptation, see (Griffiths, 1996; 1997: Ch 5; Sterelny & Griffiths, 1999: Ch 10).

neuroscientists primarily because of the need to make use of animal models for research into those causal roles.

The philosopher Karen Neander is one of the leading advocates of the view that biological and psychobiological theories are primarily theories of adaptive function and she has recently defended this view against the claims of homology (Neander, In Press). Neander argues against the suggestion by Ronald Amundson and George Lauder and myself that biological disciplines like anatomy and physiology are primarily concerned with traits defined by homology (Amundson & Lauder, 1994; Griffiths, 1994). This emphasis on homology would, of course, extrapolate to the psychological and neuropsychological versions of anatomy and physiology, as I have argued elsewhere (Griffiths, 1997: Ch. 7-8). On my reading, Neander is another philosopher who uses the fact that descriptive functional properties (e.g. causal roles) play a critical role in anatomical reasoning as evidence against the central role of homology in anatomical reasoning. But descriptive functional properties, such as biomechanical properties in anatomy or computational capacities in neuropsychology, are on a par with descriptive structural properties like bone density or neural connectivity. These descriptive properties, whether functional or structural, are the things that are judged homologous and analogous between species. The relative importance of descriptive function and structure in anatomical reasoning is a completely separate issue from the relative importance of adaptive function and homology. Thus, for example, Neander argues that “in some systems of systematics ... evidence about function is taken into account in determining homology. ... Thus, sometimes, an inference to function is prior to an inference to homology” (Neander, In Press: xxx). If ‘function’ here means descriptive function, then her observation is uncontroversial and is consistent with the views of Amundson and Lauder and myself. But if it means adaptive function, then the claim must be false. To have an adaptive function is to be a member of a lineage of copies that has a history of selection. It is relatively easy in most taxa to define a lineage of whole organisms, because organisms give birth to other organisms. Traits of organisms, however, do not give birth to little traits and so they do not form lineages except as corresponding parts of ancestor and descendant, that is, as homologues. It is easy to forget this, and to suppose that ‘corresponding part’ is a simple, observational notion. After all, the judgment that the primary flight feathers in some almost flightless breeds of white domestic duck correspond to the primaries in other birds and thus that it is their function to provide lift seems to be made by simple inspection. The real nature of this judgment becomes clear in more complex cases, such as judging whether the ‘whiskers’ of the kiwi are modified feathers or an evolutionary novelty, or whether part of an ovarian cyst is deformed epidermal tissue. But however obvious the correspondence, it remains true that the ‘corresponding parts’ of ancestor and descendant are their homologous parts, that it is in virtue of being homologous to the parts of ancestors that trait have histories of selection and that it is virtue of history that traits have adaptive functions. This is not to say that categories of analogy can be replaced wholesale by categories of homology! Analogies unite different homologous traits, each with its own selection history, in virtue of common features of those selection histories. As Darwin

realized, we need both the unity of type and the effect of the conditions of existence to think clearly about biological form. But ascriptions of adaptive function - of the effect of the conditions of existence - are logically dependent on prior ascriptions of homology.

### *3.2 Homology and Evolutionary Psychology*

Homology as an organizing principle for the study of the mind has enormous potential but has hardly been exploited in Evolutionary Psychology. I will not attempt here to convince those who are, on general grounds, sceptical of the heuristic value of evolutionary thought for psychology. I will only suggest that if what is wanted is an evolutionary heuristic for psychology, and particularly neuropsychology, then there are a number of reasons why psychological traits defined by evolutionary homology may be better targets for scientific study than psychological categories defined by evolutionary analogy. The first reason is that assignments of homology are less epistemically demanding than assignments of adaptive function. This is surely a good reason to use classifications based on homology wherever possible; working on categories that are hard to establish firmly and whose membership consequently tends to fluctuate with changes in theory is simply inconvenient. I am concerned not to be seen as defending the position, sometimes seen in the literature on ‘anti-adaptationism’, that almost nothing can be known about the adaptive, evolutionary function of traits. In many cases well-confirmed knowledge of adaptive function can be obtained, typically by the use of comparative methods. I will argue, however, that philosophers of mind and Evolutionary Psychologists have erred in the other direction, supposing that reasonable estimates of adaptive function can be obtained with surprisingly little work and even that knowledge of adaptive function is easier to come by than knowledge of homology, a position that I take to be logically incoherent for the reasons given above.

One reason why assignments of adaptive function are epistemically demanding was extensively discussed in section two of this paper. The idea that the mind has been shaped by a set of independently defined problem in the ‘environment of evolutionary adaptedness’ ignores the co-evolutionary relationship between niche-structure and phenotypic structure. The less we know about a phenotype, the less we know about the parameters of niche-space that constitute the selective environment of that phenotype. Thus, our ability to infer the adaptive pressures that shaped the human mind will be proportional to our understanding of the human mind. This severely undermines the potential of ‘adaptive thinking’ as a heuristic method for defining complex mental functions we do not yet understand.

This reservation about ‘adaptive thinking’ does not speak directly to the question of the *relative* difficulty of classifying by adaptive function or by homology. A second argument, however, speaks very directly to this issue. As I discussed briefly above, it is extremely difficult to test adaptive hypotheses without knowing where the adapted trait and other traits to which it is functionally related fit into the comparative pattern, that is,

without knowing to what they are homologous. Since homology is assessed either from background knowledge of relatedness (today often derived from molecular systematics) or by the traditional operational criteria described below, knowledge of homology does not depend on knowledge of adaptive function. Hence, while homology can typically be determined in ignorance of adaptive function, assignments of adaptive function in ignorance of the relevant facts about homology are almost untestable.

Amundson and Lauder have claimed that assignments of homology are less epistemically demanding than assignments of adaptive function for a third reason, one that has been disputed by Neander (Amundson & Lauder, 1994). She rejects their claim that homology is a more ‘observational’ and less ‘inferential’ concept than adaptive function, remarking that:

“It would be hard to choose between function and homology as to which of them was more or less inferential or observational. In order to determine homologous relations, we have to make inferences about evolutionary history, just as we do when we determine normal [*adaptive*] functions.”(Neander, In Press: xxx)

What Neander says is quite correct, but Amundson and Lauder are not likely to have forgotten that the Darwinian homology concept is defined in terms of common descent. Their point as I understand it is that homology is a highly operational concept and that the operational criteria for judging homology carry a great deal of weight when compared to its theoretical definition. In fact, there is good reason to suppose that if future empirical findings place the operational criteria of homology in conflict with the current theoretical definition of homology (Darwinian homology), then ‘homology’ would continue to refer to whatever turns out to be the property picked out by the operational criteria<sup>8</sup>. Thus, judgments of homology tend to be relatively stable in the light of evolving background knowledge. The operational criteria of homology were developed by the great descriptive embryological tradition of the first half of the nineteenth century. Richard Owen’s definition of a homologue, “The same organ in different animals under every variety of form and function.” (Owen, 1843: 374), was given at a point where the theoretical definition of homology was exceedingly obscure. Owen himself offered a theory of ‘archetypes’, while his contemporary Karl Ernst von Baer explained homology in terms of shared developmental potentials in the egg. The inability to agree on a theory of homology did not prevent early C19 biologists from developing the criteria of homology to the point where strong scientific consensus could be established on even subtle, distant homologies. Thus, well before Darwin dared announce his theory in public, some of its most powerful supporting evidence had already been established as biological orthodoxy. M.H Rathke had demonstrated the homology between the hyoid bone in animals and the gill arches in fish, for example, and von Baer had identified the notochord - the homologous structure that defines the chordates and from which the backbone develops

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<sup>8</sup> Some philosophers would put this point by saying that Darwinian homology is the ‘secondary intention’ of the homology concept, whilst Remane’s criteria are its ‘primary intention’.

in vertebrates. The criteria they used, most notably relative position in the embryo, have remained orthodox to the present day and can be found in Remane's famous codification of criteria of homology (Remane, 1952). The concept of Darwinian homology is therefore best conceived as a Darwinian explanation of the *phenomenon* of homology: the existence of 'corresponding parts' is explained by descent from common ancestors. This interpretation is strongly reinforced by current theoretical debates over the definition of homology<sup>9</sup>. The evolutionary developmental biologist Gunther Wagner has argued that the Darwinian concept has no account of what makes a part of a parent homologous to a part of an offspring and merely relies on the traditional criteria of homology to specify this relationship (Wagner, 1994). Wagner calls for the development of a 'biological homology concept' that would define homology in terms of the developmental mechanisms that generate correspondences between parent and offspring. Another criticism of the Darwinian homology concept is that it does not apply straightforwardly to serial homologues, since these homologous parts of a single organism, such as vertebrae, need not share a common ancestor even in the extended, embryological sense of 'ancestor'. Proposals to capture the phenomenon of serial homology by defining homologues as characters caused by the same biological information are perhaps best regarded as promissory notes for Wagner's 'biological' (e.g. developmental) homology concept, since the only operational definition that that could correspond to this proposal at present would define homology in terms of shared gene expression and this is clearly inadequate. Traits that are not homologous can be built from the same genes and homology at the morphological -and presumably behavioral - level can be identified even when the genes involved in the relevant developmental pathways have been substituted by evolutionary change. These proposals to redefine homology have a striking feature. They take the operational criteria of homology as firm ground to stand on whilst arguing for radical revision in the theoretical definition of homology.

I have been arguing that homology has well-established operational criteria and that it is a relatively theory-independent phenomenon. Hence, classifications in terms of homology are stable across changes in background theory. This is an obviously desirable property for categories that one science (psychology) is going to borrow from another (biology) in the hope of getting an external guarantee that nature is being carved at its joints. But enthusiasts for adaptive function can point to their own pre-theoretical phenomenon - the apparent design of many traits in relation to the organism's way of life. The tradition of natural theology identified design is a manifest fact that cried out for explanation and the scientific biology of design - Cuvier's 'law of the conditions of existence' - was well established before Darwin came along. It is arguable, however, whether the study of design before Darwin had generated a definitive methodology for assigning purposive functions to the parts of animals and still more arguable whether assignments of purposive function have exhibited since that time the same sort of stability as assignments of homology. Darwinians agree with natural theologians that traits show evidence of design, but they frequently disagree about what they are designed for:

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<sup>9</sup> For a summary, see (Brigandt, In Press).

Richard Dawkins and John Paul II have rather different views on the proper function of sex. More seriously, contemporary Evolutionary Psychologists reject many of Konrad Lorenz's views about the function of specific behaviors - 'aggression' being a famous example. The persistent tendency of twentieth-century biology to redefine 'adapted' to mean 'the product of natural selection' and to internalize this redefinition to the point where the older concept is almost forgotten (Godfrey-Smith, 1999) also suggests that, unlike homology, adaptive function is a concept for which current theory takes precedence over old operational criteria. Ultimately, however the fate of Amundson and Lauder's claim that assignments of function are more 'inferential' than assignments of homology probably turns on the diffuse and hard to evaluate claim that assignments of adaptive function fluctuate more markedly than assignments of homology with changes in theory and with new factual discoveries. I am inclined to agree with them, but to establish this would take a very extensive review of specific cases, which I will not attempt here.

### *3.3. The Argument from Causal Depth*

I have considered three arguments for the view that assignments of adaptive function are more epistemically demanding than assignments of homology. But even if this were established, it would only be a subsidiary argument for the more general conclusion that homology should be the prime classificatory principle for psychology, and particularly for neuropsychology. The main argument for this conclusion is what might be called the 'argument from causal depth'. Categories of analogy group together traits that resemble one another in the causal role they fulfill. Categories of homology group together traits that resemble one another in the underlying mechanisms with which they fulfill one of more causal roles. Psychology is concerned to discover the mechanisms by which tasks are performed and there are typically several ways to perform a task. Hence homology groups like-with-like in the respects relevant to psychology. Neuropsychology is the discipline amongst the sciences of the mind in which the premisses of this argument are most obviously correct, and hence in which it carries most weight. I have presented this argument at length in other publications, so I can be relatively brief here (Griffiths, 1994; 1997: Ch. 7-8; 1999).

For the most basic forms of scientific inference to be valid, they must be applied to 'natural kinds', categories that correspond to some inherent structure in the subject matter and not merely to the whim of the person classifying. The very idea of repeating an experiment, for example, presumes that the new subjects are 'of the same kind' as the old. Extrapolation from samples presumes that there are other things 'of the same kind' as the samples. The fundamental property that underlies these and other scientific inferences is 'projectibility': the existence of some grounds for supposing that correlations between the different properties of the samples can be 'projected' onto unexamined members of the category (Goodman, 1954). Thus, for example, chemical elements are projectible with respect to their chemical properties. If a sample of gold dissolves in *aqua regia*, probably other samples will too. The grounds for projecting

observations made on samples of chemical elements used to be merely empirical: chemistry conducted in this manner was highly successful. Today there are deeper reasons in physical theory for supposing classification by atomic number to define natural kinds for the purposes of chemistry. But chemical elements, although the traditional flagship example of natural kinds, turn out to be a rather restrictive special case. In many sciences, extrapolations of even the most sensible kind from the best possible data are not 100% reliable. No one supposes, for example, that even the best diagnostic categories in medicine will allow deterministic predictions of treatment outcomes. Hodgkins lymphoma is nevertheless a very useful category in oncology. So this aspect of the traditional model of natural kinds needs to be relaxed. 'Naturalness' is a matter of degree, and any category that allows better than chance predictions to be made from samples to unexamined instances has some degree of naturalness. Science seeks natural kinds, and the more natural the better, but it settles for the best available in the domain being investigated. Another unusual feature of chemical elements is that being 'of the same kind' is a matter of sharing an intrinsic structure. This requirement needs to be relaxed in the life sciences. Species are natural kinds for the purposes of many sciences - anatomy, physiology, molecular biology and psychology, amongst others. Findings about one rat can reliably be projected onto other rats. Since the modern synthesis, however, it has been accepted that natural populations are pools of variation, that they are continually evolving and consequently that it is futile to try to define species in terms of a common intrinsic structure. Instead, we explain the projectibility of species categories by the fact that members of a species are part of a pattern of ancestry and descent. The members of a species inherit many shared features, and interbreeding and ecological forces ensure that species members at any one time are all very similar.

Different categories are projectible with respect to different domains of properties. Both analogies and homologies are projectible categories, but only with respect to the specific domains of properties that biological theory links to them. Analogous traits share a common function, so discoveries about what it takes to perform that function can be projected from a trait in one species to analogous traits in other species. Categories of analogy are thus suited to the study of the process of adaptation. Optimal foraging theory, for example, can be tested on any organism that forages, whether it is a bird, a mammal or a snake. If the theory is confirmed, it can be applied to other foragers with increased confidence. In contrast, homologous traits need not share a function, but they do share a common ancestor. Homologues are modified forms of a single, ancestral trait. Because parents resemble their offspring in the whole gamut of functional and structural properties, discoveries about a very wide range of properties can be projected from a trait in one species to homologous traits in other species. This is why anatomy and physiology are structured around categories of homology. We expect discoveries in morphology, biomechanics, physiology, biochemistry and a host of other domains to be projectible from one snake to another snake with reliability proportional to the taxonomic distance of the two species in a phylogeny of the squamata.

If these considerations are applied to the study of psychology and neuropsychology, the ‘argument from causal depth’ emerges automatically. Suppose two animals have psychological traits that are analogous - perhaps they are both mechanisms for predator detection. Then we should expect both performances to look like a solution to a signal detection problem (Godfrey-Smith, 1991). For example, we might expect sensitivity (the probability of making type II errors) to be a positive function of the value of the tasks the organism is engaged in while it monitors for predators. All that follows, however, about the computational processes which evaluate the relevant noise/signal ratios or whatever surrogate measure the organism uses, is that their output will approximate the optimal phenotype predicted by signal detection theory. Even less follows about how the relevant computations will be realized in the animal’s brain. Some prominent Evolutionary Psychologists have arrived at these conclusions independently by reflecting on the relationship between David Marr’s ‘levels of analysis’ in cognitive science and the theory of natural selection:

“When applied to behavior, natural selection theory is more closely allied with the cognitive level of explanation than with any other level of proximate causation. This is because the cognitive level seeks to specify a psychological mechanism’s function, and natural selection theory is a theory of function.” (Cosmides & Tooby, 1987: 284)

In contrast to this case of analogy, suppose that two animals have psychological traits that are homologous - the basic emotion of fear in humans and fear in chimpanzees, for example. We can predict that, even if the function of fear has been subtly altered by the different meaning of ‘danger’ for humans and for chimps, the computational methods used to process danger-related information will be very similar and the neural structures that implement them will be very similar indeed. After all, Joseph LeDoux’s widely accepted account of fear processes in the human brain is largely, and legitimately, based on the study of far more distantly homologous processes in the rat (LeDoux, 1996). Inferences to shared mechanism based on homology are not 100% reliable, but they are reliable enough to build good science with, and, what matters in this context, they are more reliable than inferences to shared mechanism based on analogy.

The argument from causal depth seems to me hard to evade. Psychology is in the business of uncovering the mechanisms that produce behavior. This is even more evident in the case of neuropsychology. Hence these disciplines seek categories that are heuristically valuable for the study of underlying mechanisms. It is a truism in comparative biology that similarities due to analogy (shared adaptive function) are ‘shallow’. The deeper you dig the more things diverge. Bat wings and bird wings have similar aerodynamic properties but their structure diverges radically, despite their deep homology as tetrapod limbs. In contrast, similarities due to homology (shared ancestry) are notoriously deep - even when function has been transformed, the deeper you dig the more similarity there is in mechanisms. Threat displays in chimps look very different from anger in humans, but the more you understand about the facial musculature, the

more similar they appear. The same is almost certainly true of the neural mechanisms that control them. The only reason to suppose that psychology is different from morphology is to suppose that, unlike anatomical functions, psychological functions can only be realized by one set of computations and those computations can only be realized by a single neural architecture. With a few prominent exceptions, that claim is highly implausible.

## 6. Conclusion

I have contrasted three concepts of modularity: developmental, functional and mental modularity. Developmental modules are the parts of a semi-decomposable developmental system. Functional modules are the parts of a semi-decomposable phenotype, such as a neural architecture. Mental modules are ‘virtual modules’ - aspects of an organism’s psychological performance profile that can be developmentally and functionally dissociated from one another in such a way as to allow performance in one domain to be optimized independently of performance in the other. This may or may not be because the mental module maps simply onto one or more functional modules. Hence, neuropsychology and Evolutionary Psychology may not recognize the same list of modules. The same may be true of mental modules and developmental modules, but I have not attempted to establish this here. I have, however, argued that an adequate account of the relationship between modularity and adaptation must recognize a co-evolutionary process in which the organism’s capacity to developmentally dissociate performances is part of what makes separate adaptive problems ‘separate’ whilst the existence of separate adaptive problems influences the evolution of developmental modules.

I have commented on the neglect of homology as a principle of categorization, both in Evolutionary Psychology and in the philosophy of psychology. I presented three arguments suggesting that the assignment of homology may be less epistemically demanding than assignments of adaptive function. Categories of homology imported into psychology for the purpose of getting an external guarantee that nature is being ‘carved at its joints’ are therefore more likely to be stable than categories of analogy. Stable categories are surely to be preferred to unstable ones for this purpose. More definitively, the ‘argument from causal depth’ provides a powerful reason to prefer homology to analogy for the purposes of psychology, and particularly neuropsychology. Extrapolation of experimental results in neuropsychology to homologues of the experimental system are warranted, but similar extrapolations to analogues are not warranted. The most fundamental scientific inferences - such as induction - are thus warranted in one case and not in the other.

My aim in his paper was to explore the potential value of the central themes of evolutionary developmental biology for the study of psychology from an evolutionary perspective. I hope I have succeeded in convincing at least some readers that these themes could prove as revolutionary in the study of psychology as they have already proved in the study of morphology.

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