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The phylogeny fallacy and the ontogeny fallacy

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Abstract In 1990 Robert Lickliter and Thomas Berry identified the *phylogeny fallacy*, an empirically untenable dichotomy between proximate and evolutionary causation, which locates proximate causes in the decoding of 'genetic programs', and evolutionary causes in the historical events that shaped these programs. More recently, Lickliter and Hunter Honeycutt (Psychol Bull 129:819–835, 2003a) argued that Evolutionary Psychologists commit this fallacy, and they proposed an alternative research program for evolutionary psychology. For these authors the phylogeny fallacy is the proximate/evolutionary distinction itself, which they argue constitutes a misunderstanding of development, and its role in the evolutionary process. In this article I argue that the phylogeny fallacy should be relocated to an error of reasoning that this causal framework sustains: the conflation of proximate and evolutionary explanation. Having identified this empirically neutral form of the phylogeny fallacy, I identify its mirror image, the *ontogeny fallacy*. Through the lens of these fallacies I attempt to solve several outstanding problems in the debate that ensued from Lickliter and Honeycutt's provocative article.

Keywords Phylogeny fallacy · Ontogeny fallacy · Evolutionary psychology · DST · Genetic program

Introduction

Biological explanations are commonly divided into those that are 'proximate' and those that are 'evolutionary', or 'ultimate'. Proximate explanations focus on causes in the present; evolutionary explanations focus on how the present has been shaped by events in the past. Lickliter and Berry (1990) argue that this framework gives rise to

the *phylogeny fallacy* when proximate factors and evolutionary factors are understood as alternative *causes* of development.

Taken out of its usual context the term 'evolutionary cause' is an oxymoron. Evolutionary history is not a causal agent, acting in the present. Mayr's (1961; 1982) influential definition of the proximate/evolutionary distinction avoids this implication. On Mayr's definition, proximate causes have to do with the decoding of 'genetic programs' and evolutionary causes have to do with the historical events responsible for the contents of these programs. Evolutionary causes determine the contents of genetic programs; proximate causes determine their expression.

Lickliter and Berry argue that this dichotomous causal framework, with its appeal to genetic programs, constitutes a fallacy. The fallacy can be traced to a bad assumption; that development is guided by a 'genetic program' which has been selected for over evolutionary time. This assumption, they argue, is questionable in light of current biological knowledge. At best, appeals to genetic programs are promissory notes to be redeemed by future biology. At worst, the genetic program concept constitutes a deep misunderstanding of development, and its role in the evolutionary process.

Lickliter and Honeycutt (2003a) have argued that the phylogeny fallacy is endemic to Santa Barbara-style Evolutionary Psychology (EP), as formulated by Jerome Barkow, Leda Cosmides and John Tooby in their manifesto *The Adapted Mind* (1992). They argue that Evolutionary Psychologists' use of the genetic program concept, and also the modularity concept, is bound up with the fallacy. Lickliter and Honeycutt advocate a new evolutionary psychology research program, which would reject the proximate/evolutionary distinction and adopt developmental systems theory (DST) as its conceptual framework, thereby avoiding the phylogeny fallacy.

Lickliter and Honeycutt's paper was a target article. The respondents, who together formed a sort of EP 'dream team', included David Bjorklund (2003), David Buss and H. Kern Reeve (2003), Charles Crawford (2003), Dennis Krebs (2003), and Tooby, Cosmides and Clark Barrett (2003). Their replies held some surprises. One of the common criticisms – levelled by Bjorklund, Crawford, and Krebs – was that Lickliter and Honeycutt's proposed program is, in some sense, *not evolutionary*. Yet how could Lickliter and Honeycutt have added all of the ingredients to their new research program for evolutionary psychology but have forgotten to include evolution? What was most surprising about the replies, however, was that only one

respondent, Bjorklund, even mentions the phylogeny fallacy. As Bjorklund correctly points out, "Most of the criticism Lickliter and Honeycutt (2003) bestowed on evolutionary psychology is related to the *phylogeny fallacy*" (2003, 838; italics in the original). Something has clearly gone wrong when only one of the critical replies to a target article addresses its main argument.

In this paper I revise the phylogeny fallacy to ensure that it will not be so easily overlooked. Lickliter and Berry's argumentative strategy is to refute the gene-centred biology that gives rise to the phylogeny fallacy and to present DST as its antidote. Recognition of the phylogeny fallacy is thus tantamount to a theoretical conversion to DST. However, if one is not convinced by DST one will not be convinced that the phylogeny fallacy is a genuine fallacy. If the phylogeny fallacy is to act effectively as a regulative principle in the biological sciences it should not be so closely tied to any particular biological school of thought. I suggest that we should relocate the phylogeny fallacy from Mayr's dichotomy between proximate and evolutionary *causation*, with its use of the genetic program concept, to the more fundamental conflation of proximate and evolutionary *explanation*, which Mayr's framework sustains. To offer an evolutionary explanation of a trait, and then to claim that its development is explained by an evolved genetic program *without* offering supporting proximate analysis is to conflate proximate and evolutionary explanation. The basic problem here is one of explanatory conflation: the value of the genetic program concept is a secondary issue.

By way of a revised definition, the phylogeny fallacy is committed when a proposed proximate explanation is no more than an evolutionary explanation in disguise. Having thus defined the phylogeny fallacy, I identify its counterpart – its mirror image – in the *ontogeny fallacy*. The ontogeny fallacy is committed when a proposed evolutionary explanation is a proximate explanation in disguise. Just as population-level evolutionary analysis alone cannot explain development and form, development and form alone cannot explain population-level phenomena.

Here is the agenda for my paper. In the following section I discuss the phylogeny fallacy, and make the case for my revised definition. I identify two forms of the fallacy: one causal, the other developmental. In the next section I argue that Evolutionary Psychologists commit this fallacy, and I offer a tentative explanation for the lack of discussion of the phylogeny fallacy in the critical replies. Then I turn to Lickliter and Honeycutt's proposal for a new evolutionary psychology, and I

reconcile the disagreement between them and their respondents about the status of their program as a form of *evolutionary* psychology. In the final section before the conclusion I argue that Lickliter and Honeycutt's proposed research program, whilst avoiding the phylogeny fallacy, would commit the inverse fallacy, the ontogeny fallacy.

The phylogeny fallacy revisited and revised

Lickliter and Berry (1990) associate the phylogeny fallacy with Mayr's formulation of the proximate/evolutionary distinction. The genetic program concept plays a central role in Mayr's framework: genetic programs being the supposed storehouses for all of our species-specific developmental information. According to Mayr, both proximate causes and evolutionary causes have to do with genetic programs:

> Organisms, in contrast to inanimate objects, have two different sets of causes because organisms have a genetic program. Proximate causes have to do with decoding of the program of a given individual; evolutionary causes have to do with the changes of genetic programs through time, and with the reasons for these changes. (Mayr 1982, 68)

For Mayr, development and behaviour are reducible to the 'decoding of genetic programs' (proximate causation), the contents of which are explicable in terms of the evolutionary forces that shaped them (evolutionary causation).

Lickliter and Berry argue that Mayr's causal framework constitutes a fallacy because "it assumes (often implicitly) that behind the phenomena of development lie the genes as ultimate causal factors; therefore, development is (at least to some extent) simply the manifestation of genetic information about evolved (phylogenetic) characters" (1990, 353). Against this predeterministic account of development, which sees phenotypes as somehow preformed in genetic instructions, they argue that genes are but one (albeit an important one) of a complex of internal and external resources that interact to produce developmental outcomes – both plastic and robust – in a process that has no single locus of control. In other words, they advocate DST (to which we shall return).

Celia Moore's work on masculine sexual behaviour in rats highlights some of the problems with the genetic program concept. Moore (1984; 2007) has shown that the penile reflex in rats depends on gene expression in the spinal cord nuclei of rat pups. Yet we cannot infer that it is therefore 'genetically programmed'. The expression of these genes is the result of the mother licking the pup's genital area (Moore 1984; 2007). These genes are not constitutively expressed; their expression depends on the licking. The mother preferentially licks the male pups due to a chemical attractant in their urine. The transgenerational reconstruction of the ability of male rats to copulate is so reliable that it certainly appears programmatic. Yet, given what we know about the development of the penile reflex in rats, appealing to a program in the genome that contains information about the ontogenetic pathway of this trait would be ad hoc, question begging, and redundant.

A causal framework that contrasts a 'genetic plan' with the environmental vicissitudes it undergoes necessarily overlooks the co-constructive nature of development. The 'environment' – everything that is not a gene – becomes a trigger, a facilitator, or a disruptor to genetic programs. The problem with this causal framework therefore lies as much in its dichotomising of a system as it does in its predeterminism and preformationism (Lickliter & Berry 1990, 355). Furthermore, Lickliter and Berry argue that use of the genetic program concept "can and often does lead to the belief that the process of development is thereby somehow explained or understood, eliminating the need for any further investigation or research" (1990, 354). They associate the distinction between proximate and evolutionary causation with a sidestepping of development. In fact, Lickliter and Berry identify so many problems with this causal distinction that they identify the fallacy with the distinction itself, rather than any particular error of reasoning that it produces.

When it appears in an argument, the phylogeny fallacy often looks something like this:

1. Adaptive pressures in species X are thought to have led to the evolution of adaptation A
2. The development and behaviour of members of species X is consistent with the existence of adaptation A

3. The instructions for the construction of phenotypic adaptations in species X are stored in its evolved genetic programs, and the environment acts, variously, as a trigger, facilitator, or a disruptor to these programs

C. The construction and functioning of adaptation A in members of species X can be explained by reference to their genetic programs (evolutionary causation) in interaction with their environments (proximate causation)

The argument above is an instance of the phylogeny fallacy because it relies on the distinction between proximate and evolutionary causation, implicitly introduced in premise 3. As I have indicated, Lickliter and Berry explore a host of problems with this causal framework. However, we can trace these back to a core problem that this framework sustains: the conflation of proximate and evolutionary explanation.

Notice that the conclusion of the argument above does not follow from its premises. At no stage has the proximate mechanism – the genetic program – been described. The leap from plausible evolutionary story to proximate mechanism is a leap of faith. This amounts to a conflation of proximate and evolutionary explanation. The conclusion of the argument makes a claim about a proximate mechanism, a genetic program dedicated to a phenotypic adaptation, but this seemingly proximate explanation *has no proximate explanatory content*. There is no premise 4 that describes the genetic program (showing that it exists, how it works, etc.). We are actually being offered an evolutionary explanation for why the trait should be considered an adaptation, rather than a proximate explanation concerning the mechanisms underlying it. The gesturing towards the genes is empty, even though the reference to the genes appears to be doing the explanatory work.

Proximate explanations must contain proximate content. To offer a proximate genetic explanation that uses genetic terms metaphorically to express an evolutionary theory is to conflate proximate and evolutionary explanation. I suggest that we should associate the phylogeny fallacy with the conflation of proximate and evolutionary *explanation*, rather than with the use of Mayr's dichotomy between proximate and evolutionary *causation*. The former identifies a logical problem, the latter an empirical problem (regarding the existence and functioning of genetic programs).

It is important to note that if the phylogeny fallacy as described by Lickliter and Berry is indeed a fallacy, its instances will involve a conflation of proximate and

evolutionary explanation. If this were not the case, and some explanations appealing to genetic programs were genuine proximate explanations, describing how programs direct development and behaviour, then the phylogeny fallacy would be refuted. Mayr's causal framework would be vindicated. For this reason the conflation of explanatory types is a more fundamental problem than the causal dichotomy Lickliter and Berry criticise.

Another reason to associate the phylogeny fallacy with the conflation of proximate and evolutionary explanation is that the fallacy, as described by Lickliter and Berry, is excessively informal. Their 1990 article is an extended argument for the very existence of the phylogeny fallacy by showing how the assumptions they associate it with are untenable in the light of empirical studies in developmental and evolutionary biology. To invoke the fallacy requires either an appeal to their authority or a reproduction of their lengthy argument, along with the scientific citations necessary to make the argument good. The first strategy is undesirable, given the controversial nature of the debate; the second strategy is unwieldy, and many will not be persuaded that a fallacy has been identified. On the other hand, I assume it to be uncontroversial that conflating proximate and evolutionary explanation is a mistake. Unless otherwise indicated, I shall use the 'phylogeny fallacy' to refer to this conflation.

We can reformulate the fallacy using Nikolaas Tinbergen's (1963) four-question approach, which identifies two kinds of proximate explanation, and two kinds of evolutionary explanation (Griffiths 2009). Tinbergen distinguished four questions we could ask concerning why an animal exhibits a particular behaviour. (1) *The question of causation.* What mechanisms underlie the trait? (2) *The question of survival value.* What role does the trait play in survival and reproduction, and could survival and reproduction be better promoted by changes in the trait? (Tinbergen 1963, 418) (3) *The question of ontogeny.* How does the trait develop? (4) *The question of evolution.* What has been the course of the trait's evolution, and why has this evolutionary course spread the trait as we observe it today? (Tinbergen 1963, 428) Questions 1 and 3 are proximate; questions 2 and 4 are evolutionary. The question of survival value is a forward-looking evolutionary question, asking what evolutionary forces currently act on the trait (Griffiths 2009).

We can now identify two forms of the phylogeny fallacy. One form relates to the question of causation: it is the conflation of the question of causation with the

question of evolution (or more precisely, the part of the evolutionary question that asks *why* the trait evolved). The other form arises from the conflation of the question of ontogeny with the question of evolution (again, with the part that asks why the trait evolved). In the former, what appears to be a causal explanation is actually a disguised evolutionary explanation. In the latter, an apparently developmental explanation turns out to be an evolutionary explanation in disguise, with little or no proximate developmental content.

To complement Lickliter and Berry's empirical arguments against Mayr's causal framework, we can now provide a more basic criticism, drawing on a simple observation: that while molecular developmental biology is gene-centred, it does not involve identifying and decoding programs in the genome. This fact, which is often either taken for granted or overlooked, has some important consequences. It makes the language of proximate analysis in Mayr's description of the proximate/evolutionary distinction misleading. The claim that an organism develops or behaves in a certain way because of its genetic program is always made in absence of any proximate analysis of the inferred program. Lickliter and Honeycutt hint to this when they note that for Evolutionary Psychologists "the genome is an object of reference, it is not an object of study" (2003b, 868). Claims about genetic programs are made on the basis of evolutionary analysis (inspired by functional analysis) rather than proximate analysis of programs themselves (as one might assume). As an evolutionary explanation of a trait does not provide grounds for a proximate explanation of that trait, to infer the latter from the former is to *conflate* proximate and evolutionary explanation, and to commit the phylogeny fallacy.

While I am sympathetic to the DST approach endorsed by Lickliter and Berry, all I need to make my argument good is to point out that genetic programs are not objects of study (and therefore serve only as token proximate explanations). I take the following to be uncontroversial. The genetic program concept is deduced from the framework of the modern synthesis, not discovered by geneticists who map genetic blueprints for phenotypes. No such maps exist. No such geneticists exist. That is not to say that there is no genetic code; the DNA base sequences in a gene's coding regions are the blueprint for the amino acid sequence in the primary structure of one or more proteins. However, nobody has discovered a gene to phenotype code, which is what the genetic program is supposed to be.

Use of the genetic program concept can give rise to both the causal and the developmental form of the phylogeny fallacy. In the causal form, the genetic program poses as a mechanical explanation for how a trait performs its function. In the developmental form, the program is used to 'explain' ontogeny. Importantly, for either form of the fallacy to take place the program must be inferred primarily through evolutionary thinking. Otherwise the problem is not one of explanatory conflation but simply of pseudo explanation.

One possible response to my interpretation of the phylogeny fallacy would be to argue that 'genetic programs' are merely promissory notes that are expected to be redeemed by future biology, and that those who appeal to them understand that they are merely token proximate explanations. My point is simply that this must be made explicit. It should be clear when what is being offered is a prediction, rather than a description of an object of study. The phylogeny fallacy – as I have defined it – is an important fallacy to uncover because talk of proximate mechanisms in evolutionary biology makes it sound like the science describing these mechanisms has already been done. Instances of the phylogeny fallacy show that this is not always the case. Let us move on now to discuss the phylogeny fallacy in relation to EP.

EP: a case study

Evolutionary Psychologists propose that natural selection, when faced with a problem, tends to produce a fairly specific solution. Bladders store urine; lungs deliver oxygen to, and remove carbon dioxide from, the blood. We have no 'general purpose organs'. Our brains are no exception. They are not blank slates. Just as the body has many organs, Evolutionary Psychologists argue that the brain has "hundreds or thousands" of special purpose organs, which they call *mental modules*, or *mental mechanisms* (Cosmides & Tooby 1995, 1189). Drawing on Jerry Fodor's (1983) *The Modularity of Mind*, Evolutionary Psychologists characterise modules as specialised information-processing mechanisms that we have evolved to deal with adaptive problems in our ancestral past. As the theory and methods of EP have been well rehearsed elsewhere (e.g. Cosmides & Tooby 1995; Sterelny 1995; Laland & Brown 2002) I will not continue to detail them here.

Before I ask whether Evolutionary Psychologists commit the phylogeny fallacy in

the sense I described in the previous section, I will support Lickliter and Honeycutt's (2003a) claim that Evolutionary Psychologists commit the fallacy as defined by Lickliter and Berry, and explore why this criticism fell on deaf ears.

Reference to key proponents of EP suggests that Lickliter and Honeycutt's criticism is well founded:

> The mind is organized into modules or mental organs, each with a specialized design that makes it an expert in one arena of interaction with the world. The modules' basic logic is specified by our genetic program. (Pinker 1997, 21)

> The individual organism, fixed at conception with a given *genetic endowment regulating its developmental programs*, encounters its specific ontogenetic environment, which it processes as a set of inputs to these developmental programs. In other words, the organism blindly executes the programs it inherits, and the ontogenetic conditions it encounters serve as parametric inputs to these programs. (Tooby & Cosmides 1990, 388, italics added)

For Evolutionary Psychologists our development and behaviour is explicable in terms of our evolved, genetically regulated 'programs' in interaction with their environments. Tooby and Cosmides call these our 'developmental programs'. However, they are *genetic* developmental programs, as they are genetically regulated. For the program concept to make sense, the genes must be privileged as uniquely instructional. Programs are, by definition, pre-programmed. Like a computer program, a genetic program would have to have prespecified inputs and processes on which it bases its instructions. Any unspecified input would reveal a bug in the system. Tooby and Cosmides, in the quote above, acknowledge this privileged, instructional role for the genes when they describe the environment as a set of inputs to be processed by genetically regulated programs. The outputs may be context-sensitive, but the environment can only be understood to play a triggering, enabling, or disruptive role.

Lickliter and Honeycutt's claim that Evolutionary Psychologists commit the phylogeny fallacy, as described by Lickliter and Berry, is justified. Explanations in terms of genetic programs in EP appeal to the adaptive (or once adaptive) imperatives of these programs in interaction with environmental inputs. If the charge of predeterminism is not quite accurate – the outcomes of development will be co-

determined by the environment and the genes, and developmental outcomes will differ in different environments – the charge of preformationism sticks. The plans for the organism are preformed in the genetic programs it inherits. They have to be. Otherwise they would not be programs.

The difficulty with Lickliter and Berry's approach to the phylogeny fallacy is that unless one is convinced that there is something wrong with the assumptions spelled out in the preceding paragraphs one will not be convinced that a fallacy has been identified. To convince someone that the fallacy is real is tantamount to converting them to DST (or to some similar approach to biology; e.g. Gilbert & Epel's 2009 *Ecological Developmental Biology*). On the other hand, in order to reject the fallacy, one would need to reject DST. We can now attempt to answer our question concerning why only one of the five responses to Lickliter and Honeycutt's paper, Bjorklund's (2003), mentions the phylogeny fallacy.

Referring to the phylogeny fallacy Bjorklund writes, "I concur with Lickliter and Honeycutt that these assumptions are indeed false, and I argue further that they are held implicitly by most evolutionary psychologists" (2003, 838). Bjorklund, it is important to note, self-identifies as a developmental systems theorist. The other respondents could not have effectively defended themselves against the charge of the phylogeny fallacy without arguing against DST as a framework for biology. In the face of such a task, they overlooked the charge of the phylogeny fallacy, focusing on other, more specific disagreements with Lickliter and Honeycutt.

My alternative interpretation of the phylogeny fallacy offers a solution to this problem. Importantly, it is agnostic about the facts of biological processes. The observation that genetic programs are not objects of empirical study is not an argument against the existence of such programs (for this kind of argument see Sterelny 2000 or Stotz 2008). A developmental systems theorist could even commit the phylogeny fallacy if a developmental system was inferred through evolutionary analysis, without any proximate analysis of the developmental resources that supposedly constitute it. Whether development is best described by neo-Darwinists or developmental systems theorists is not relevant to my version of the phylogeny fallacy, which is not allied to any particular biological framework. The identification of the fallacy is meant to act as a regulative principle in the biological sciences; an injunction against conflating proximate and evolutionary explanation.

We can now ask whether Evolutionary Psychologists commit the phylogeny

fallacy according to my, empirically neutral, definition. As developmental biology does not describe program-like entities written in the genome, Evolutionary Psychologists are unable to describe how such programs actually work, or how they direct ontogeny. While appeals to developmental programs sound like proximate explanations, they are devoid of proximate explanatory content (beyond a gesturing towards the genes, and sometimes gene correlations). Appeals to genetic programs or developmental programs in EP are evolutionary explanations dressed up as proximate explanations, and are thus instances of the phylogeny fallacy, in my sense.

Any talk of genetic programs in EP is an instance of the phylogeny fallacy because the necessary kind of proximate analysis, the decoding of genetic instructions for gross phenotypes, is (at least at this point in time) pure science fiction. We can know a priori that any evolutionary theory appealing to genetic programs to explain phenotypes is committing the fallacy. One could ask whether biological entities might *one day* be shown to be governed by genetic programs – whether cracking the code for amino acid sequences was a step towards decoding genetic programs for gross phenotypic traits – or if the genetic program metaphor is a wildly misleading attempt to explain the often reliable transgenerational reconstruction of phenotypes by setting up a false dichotomy between genes and environments. This question, however important and interesting, distracts us from the phylogeny fallacy. Even if there were such entities as genetic programs, containing the genetic instructions for phenotypes, any theory that used evolutionary thinking to infer a genetic program would need to substantiate such an inference with a proximate description of the *particular* program in order to avoid the phylogeny fallacy.

Genetic programs are not the only proximate mechanisms appealed to by Evolutionary Psychologists. In EP the task of the genetic program is to specify the logic of a mental module. Explanations in terms of modules can also be instances of the phylogeny fallacy, on my definition, when they are merely inferred through evolutionary analysis, without supporting proximate evidence. The neurological level of the fallacy differs from the genetic level because modules, unlike genetic programs, are objects of study. There is strong evidence, for example, for the existence of a face-recognition module, located in the fusiform facial area of the brain (Kanwisher et al. 1997). So we can look at claims about modularity and ask whether they are merely inferred through evolutionary thinking – and are thus instances of the phylogeny fallacy – or whether they are also supported by an appropriate kind of proximate

analysis.

Lickliter and Honeycutt's alternative research program for evolutionary psychology

Lickliter and Honeycutt argue that for EP to avoid the phylogeny fallacy it should "abandon the proximate-ultimate distinction in favor of an explicit concern with the epigenetic processes of development within and between generations" (2003b, 869). They explain that their alternative to EP is one of "description and experimentation with the goal of showing how one generation leads to (i.e., sets up the developmental conditions and resources for) the next" (2003b, 871). As the adoption of DST would be the key innovation of the program, I briefly outline some relevant aspects of DST in this section, and ask why some of the respondents considered the program insufficiently evolutionary, and thus unable to replace EP.

The conceptual roots of DST can be found in comparative psychologist Daniel Lehrman's 1953 critique of the concepts of 'instinct' and 'innateness'. Empirical work in this tradition continues in the field of developmental psychobiology (see Michel & Moore 1995), in which Lickliter and Honeycutt were schooled. Developmental psychobiology is the experimental study of the effects of genetic and extra-genetic factors (and their interactions) in the ontogeny of gross behavioural traits, and DST is an attempt to abstract a theoretical framework from this field (Griffiths 2006).

DST dispenses with the dichotomies of gene/environment, nature/nurture and biology/culture in favour of a concern with *developmental systems* as a whole. A developmental system consists of a matrix of resources that create a *life cycle*. A life cycle is a developmental process that can construct itself out of this matrix of resources in such a way that the cycle can be reconstructed. DST is not a theory in the formal sense. Rather, it is a theoretical framework for biology, which reconceives the relations between development, inheritance, and evolution (for a detailed account of DST see Oyama et al.'s 2001).

Developmental systems theorists do not place emphasis on development in an attempt to replace evolutionary biology. Rather, they wish to make evolutionary biology more developmentally *and* evolutionarily plausible. So it is puzzling when

Bjorklund writes,

> Evolutionary psychology cannot simply adopt a developmental systems perspective without making substantial – some would say radical – changes to its fundamental base. But I believe there is nothing inherent in a developmental systems view of life that is incompatible with an evolutionary approach to human behavior. (2003, 840)

It equally puzzling that Krebs (2003) contrasts Lickliter and Honeycutt with 'evolutionary theorists'. As DST is an evolutionary approach to biology and developmental systems theorists are well described as 'evolutionary theorists' these comments are hard to comprehend. DST has a traditionally Darwinian approach to evolution, in that evolution is understood to require variation, fitness differences, and heritability. However, DST departs from neo-Darwinist thinking in its agnosticism about both the sources of variation and the systems of inheritance. "Nature", Lehrman (1970, 28) famously argued, "selects for outcomes". It is not only genes that are 'selected for', as genes are not the only reliably inherited resource that vary and upon which selection can act. According to DST selection pressures act on the matrix of resources out of which a life cycle can be recreated – developmental systems as a whole. The fitness enhancing or reducing differences on which evolution acts may be produced by any means, as long as those differences reoccur. Developmental systems theorists thus define evolution as "change in the nature of populations of developmental systems" (Griffiths & Gray 2001, 207).

We can make sense of the claim that Lickliter and Honeycutt's proposed program is not 'evolutionary' if we turn to Crawford's remark about their "lack of population thinking" (2003, 854). This lack is not inherent to the developmental systems perspective. After all, developmental systems theorists understand evolution as "change in the nature of populations of developmental systems". However, DST does not provide the practical tools for population-level analysis. DST provides a theoretical toolkit, and its proponents must adopt practical tools – e.g. mathematical modelling tools – from elsewhere. So to interpret Bjorklund's quote above, he is saying that DST is theoretically compatible with population-level analysis, and by pointing this out he is attempting to diffuse some of the tension between EP and DST.

There is a sense in which Lickliter and Honeycutt's program both is, and is not,

evolutionary. Tinbergen's (1963, 428) characterization of the 'question of evolution' is instructive here. The question of evolution is split into two sub-questions. The first asks about the course of a trait's evolution; the second asks why this evolutionary course has spread the trait as we observe it today. The first sub-question would be answered (at least theoretically) by Lickliter and Honeycutt's proposed program, which would study the "epigenetic processes of development within and between generations" (2003b, 869). However, as Buss and Reeve point out, this program "appears designed to reveal how underlying mechanisms unfold over time not why specific psychological mechanisms and the behaviors they produce have been favored by selection over competing designs" (2003, 850). As such, Lickliter and Honeycutt's program would not answer the second sub-question. Their program would be evolutionary in the sense that phylogeny is a successive sequence of ontogenies, but it would not be evolutionary in the sense that it would not accommodate population-level evolutionary analysis. In the following section I argue that this leads Lickliter and Honeycutt to commit the inverse of the phylogeny fallacy, which I call the 'ontogeny fallacy'.

The baby and the bathwater

As a developmental psychologist, Bjorklund is aware of the lack of proximate developmental analysis in EP. "Evolutionary psychology", he argues, "needs a developmental model" (Bjorklund 2003, 837). He is in agreement with Lickliter and Honeycutt that EP should adopt DST as an antidote to the phylogeny fallacy. Where Bjorklund (and the other respondents) seem to disagree with Lickliter and Honeycutt is in their claim that EP should "abandon the proximate-ultimate distinction" (2003b, 869). Insofar as Lickliter and Honeycutt are referring to Mayr's formulation of the distinction, it should be abandoned, as it leads to the phylogeny fallacy (on Lickliter and Berry's definition it *is* the phylogeny fallacy). However, the distinction between proximate and evolutionary *explanation* does not need to be abandoned. Tinbergen's formulation of the distinction, for instance, does not lead to the phylogeny fallacy. By abandoning Mayr's (gene-centred) formulation of the proximate/evolutionary distinction, but not replacing it, Lickliter and Honeycutt throw out the baby with the bathwater.

Lickliter and Honeycutt reserve an important theoretical place for natural selection as a filter of unsuccessful phenotypes. As they write,

> variations in morphologies, physiologies, and behaviors resulting from modification in developmental processes place their possessors in different ecological relationships with their environments. If these phenotypic variations provide slight advantages in survival and reproduction, then competitors without the novel phenotype will eventually decrease in frequency in the population. (2003a, 827)

However, when they formulate their alternative to evolutionary psychology they neglect population-level thinking, advocating a program of "description and experimentation" (2003b, 869) with an apparently exclusive focus on the "epigenetic processes of development within and between generations" (2003b, 869). While DST provides a conceptual framework for understanding development, inheritance, and evolution, its practitioners must borrow tools from evolutionary biology if they want to study population-level phenomena empirically. Lickliter and Honeycutt explain that their alternative to EP would involve a multi-disciplinary integration of "genetics, developmental biology, neuroscience, psychology, and anthropology" (2003a, 829), but they make no mention of evolutionary biology. And without population-level evolutionary analysis, Lickliter and Honeycutt's proposed program could not displace EP.

In fairness, it should be noted that Lickliter and Honeycutt's focus was on their critical, rather than their constructive argument. Yet it is worth asking why they neglect population-level explanation in their proposal. It may be a case of over-emphasis on their part. For instance, Lickliter and Honeycutt focus on examples where phenotypic plasticity results in a change in the frequency of a trait within a population, rather than cases in which fitness differences between traits determine which traits spread and which decline, in which selection plays a more prominent role. However, their neglect of population-level analysis appears to be grounded in their view that, "All phenotypes have a specific developmental history that explains their emergence, and a developmental mode of analysis is the only method that has the potential to fully explicate the structures and functions of maturing and mature organisms" (Lickliter & Honeycutt 2009, 43). It appears that Lickliter and Honeycutt

assume that population-level evolutionary explanations are dispensable in light of a complete description of the epigenetic, transgenerational processes of development. Trade the word 'developmental' in the quote above for the word 'evolutionary' and you have an elegant instance of the phylogeny fallacy: All phenotypes have a specific *evolutionary* history that explains their emergence, and an *evolutionary* mode of analysis is the only method that has the potential to fully explicate the structures and functions of maturing and mature organisms. It seems that Lickliter and Honeycutt have traded one fallacy, the phylogeny fallacy, for another, which we may call the *ontogeny fallacy*.

The ontogeny fallacy is the inverse of the phylogeny fallacy. It is committed when a proposed evolutionary explanation is actually a proximate explanation in disguise. In its most basic form it involves a conflation of Tinbergen's second evolutionary sub-question which asks "why did the trait evolve?" with his proximate questions of ontogeny or causation. Stuart West and colleagues (West et al. 2011) have argued that evolutionary and proximate explanation has been conflated in this manner in the human cooperation literature, particularly in discussions of *strong reciprocity*. Strong reciprocators not only obey social norms, but punish people who violate those norms. According to West and colleagues strong reciprocity is offered as an evolutionary explanation for why cooperation is maintained in human populations, when it is in fact a proximate description of how it is maintained (notice that this is the inverse of the phylogeny fallacy). As evidence West et al. (2011) quote Bowles and Gintis suggesting that "cooperation is maintained because many humans have a predisposition to punish those who violate group-beneficial norms" (2004, 17). For West and colleagues this is a 'how' answer to an evolutionary 'why' question (and hence an instance of the ontogeny fallacy). However, the quote from Bowles and Gintis continues ", even when this reduces their fitness relative to other group members" (2004, 17). Bowles and Gintis do genuinely attempt to answer the evolutionary 'why' question in the cited article. While 'why' and 'how' questions are distinct, it is often necessary and useful to invoke proximate factors when answering evolutionary 'why' questions (Laland et al. 2011). As Bowles and Gintis offer an answer to the evolutionary 'why' question, they do not commit the ontogeny fallacy.

The form of the ontogeny fallacy that Lickliter and Honeycutt's research program would produce is different. It involves the conflation of the question of ontogeny *coupled with* the first evolutionary sub-question which asks "what was the course of

the trait's evolution?" with the second evolutionary sub-question which asks "why did the trait evolve?" In other words, it is committed when a historical sequence of ontogenetic explanations are represented, implicitly or explicitly, as an alternative to population-level evolutionary explanation. Here is an example of an argument that is an instance of the fallacy:

1. The cumulative processes of development within and between human generations has led to the evolution of a spectrum of human skin colour
2. Sol is a man with dark brown coloured skin

C. Sol's skin colour is fully explained by a developmental process in Sol and similar developmental processes in each of his ancestors

This is effectively an argument for the dispensability of population-level evolutionary explanation. If a complete developmental history is indeed all that is needed to explain form and function, population-level evolutionary explanations are superfluous, and therefore dispensable (Ariew 2003).

The argument above has an intuitive appeal, but this intuition is misleading. Even if we could explain the development of a trait, how it was inherited, and trace these explanations back to deep history, something would be left unexplained. Knowing how a trait evolved is not the same as knowing why it evolved. The intuitive appeal of such arguments lies in a preference for fine-grained explanation. Yet fine-grained information misses information at a coarser grain that is complementary, and indeed necessary, for the kind of explanations we are often after in evolutionary biology and allied fields (Matthen 2009).

Lickliter and Honeycutt implicitly privilege what Frank Jackson and Philip Pettit call fine-grained *contrastive* information over coarse-grained *comparative* information:

> One sort of information helps us to differentiate the actual world from other ways the world might have been: other possible worlds. The second sort helps us, not to differentiate the actual world from other possible worlds, but to relate it to them: to show how the actual world runs on patterns found in a

> variety of possible worlds. The first sort of information is modally contrastive, the second modally comparative. (Jackson & Pettit 1992, 15)

To illustrate this distinction Jackson and Pettit offer the example of the cracking of a flask filled with boiling water. A fine-grained account of the cracking locates the exact molecule responsible for the breaking of a molecular bond in the container. This is a contrastive explanation. It tells us that the difference-maker was none other than molecule M. At this fine grain of analysis, however, we miss important information at a higher level; the fact that the water is boiling. The explanation that "the flask cracked because the water was boiling" points to the fact that in all relevantly similar cases, boiling water will cause the glass to crack. It might be molecule M or it might be molecule W that is causally implicated, it does not matter; the flask will crack. This is a comparative explanation. Both kinds of explanation are genuinely explanatory and complementary, and we have no a priori reason to prefer one to the other (Jackson & Pettit 1992).

Returning to the skin colour example that illustrates the ontogeny fallacy, we can see that it relies exclusively on contrastive explanation. It hones in on the particularities of the case; how a unique individual developed a particular skin colour. Even if this explanation can be generalised to other people with similarly coloured skin (let us assume that they inherit similar developmental resources) it is still a contrastive explanation. It supports a particular set of counterfactuals. If a person did not inherit certain developmental resources, they would not have developed the skin colour they now have.

My argument is that evolutionary explanations that rely exclusively on contrastive explanations do not support all of the right counterfactuals. For instance, if a fair-skinned person's ancestors had lived close to (rather than far from) the equator, they would probably have dark, rather than fair skin. This counterfactual statement is not supported by contrastive explanation, yet it is supported by the literature on the evolution of skin colour (Jablonski & Chaplin 2000). Fair skin, the leading selective hypothesis suggests, is an adaptation to long dark European winters, where a lack of sun, and consequentially vitamin D, posed the threat of rickets, osteomalacia, and osteoporosis. Fair skin, which is able to absorb more sunlight and hence synthesise more vitamin D, is an adaptive response to low ultraviolet radiation. Too much UV exposure, on the other hand, is linked with embryonic neural tube defects and UV-

induced injury; hence dark, highly melanised skin has been maintained by natural selection in populations from sunny areas, as it protects against these risks.

Selective explanations, which are central to evolutionary biology, and consequently evolutionary psychology, are of the comparative variety. They tell us about patterns of similarity and difference in abstraction of how these similarities and differences are instantiated. While central to explanation in evolutionary biology, too much focus on comparative explanation can be problematic. It leads to the phylogeny fallacy, for instance, when comparative (e.g. selective) explanations are offered as evidence for the existence and workings of proximate mechanisms (e.g. genetic programs and modules) without supportive contrastive (developmental and causal) explanation.

The phylogeny fallacy and the ontogeny fallacy are both caused by the conflation of proximate and evolutionary forms of explanation. A clarification is in order here, as Tinbergen's 'question of evolution' splits into two sub-questions; an evolutionary 'why' question, which asks "why did the trait evolve?", and an evolutionary 'how' question, which asks "what was the course of the trait's evolution?" Strictly speaking, it is the conflation of proximate explanation and evolutionary 'why' explanation that gives rise to the fallacies. Lickliter and Honeycutt's proposed program would answer Tinbergen's proximate questions and his evolutionary 'how' question, but not his evolutionary 'why' question. This is a problem not because explanatory projects in biology *should* answer all of Tinbergen's questions, but rather because, as a rival to EP, the program would be committed to answering evolutionary 'why' questions. Indeed, it is often useful to focus exclusively on one kind of explanation. For instance, Brett Calcott (2009) has identified a form of evolutionary explanation that does not ask the evolutionary 'why' question: *lineage explanation*. Lineage explanations show how, through a series of modifications over evolutionary time, a phenotype can plausibly change from one state to another. As Calcott notes, lineage explanations do not invoke the population-level processes responsible for such changes. By recognising that lineage explanations focus on a different – but complementary – question to the evolutionary 'why' question, Calcott immunises his explanatory program against the ontogeny fallacy.

Tooby, Cosmides and Barrett, in their reply to Lickliter and Honeycutt, admit that they are "natural selection centered" (2003, 864). This is a problem, as it assumes one can answer the proximate questions of causation and ontogeny through answering the

evolutionary 'why' question. As evolution does not design static adult forms out of thin air, an interest in natural selection (and function) cannot be divorced from knowledge of organisation and development. Evolutionary developmental biology (evo-devo) has shown that you cannot build a realistic model of the evolution of a trait unless you understand the development of that trait. The development of rodent cheek pouches is a case in point. Most rodents have internal cheek pouches, but geomyoid rodents (such as pocket gophers and kangaroo rats) have cheek pouches external to the mouth. Research on the development of rodent cheek pouches (Brylski & Hall 1988) showed that the internal pouch is the ancestral condition, and suggested an evolutionary developmental account of the introduction of external pouches in a common ancestor. The key mechanism in the development of cheek pouches is *evagination*, the process by which a body part is turned inside out. A small change in the location of the evagination, so that it occurs at the corner of the mouth, produces an external, rather than internal pouch. This discovery, coupled with the fact that no geomyoid rodent has internal pouches, suggests that pouch externalization resulted from a simple change in the development of pouches in a common ancestor. As this example demonstrates, comparative selective explanations alone cannot explain an organism's organisation, as natural selection only explains the frequency of traits in a population, not the functional organisation of traits.

The fact that proximate and evolutionary explanations are mutually illuminating has of course been long appreciated. Elliott Sober (1984) makes this point in his discussion of R.A. Fisher's explanation of the 1:1 female to male sex ratio. Fisher (1930) noted that the human sex ratio seems to deviate from this common evolutionarily stable strategy, as more boys are born than girls. However, he maintained that humans are not a counterexample to the 1:1 equilibrium. As Fisher's argument is that parents should, in order to maximise their number of grandchildren, invest equally in male and female offspring, it makes sense to have more fertilizations by Y-bearing sperm, as boys have higher prenatal and postnatal mortality rates than girls, and consequentially receive (on average) less parental investment. Sober observes that it is possible to give exclusively evolutionary or proximate explanations for the human sex ratio. His worry about this is a different, but related one to mine. Sober argues that evolutionary arguments *presuppose* knowledge about the physical properties of populations. It is impossible to give a selective argument for the uneven sex ratio in humans, he points out, without knowledge of fertilization rates and

mortality rates. My worry is that evolutionary theories (such as Fisher's), supported by knowledge about properties of populations (such as functional profiles), do not provide a basis by which we can infer the proximate causes behind phenomena of interest. To claim that they do is to commit the phylogeny fallacy.

If evolutionary psychology were to exclusively privilege contrastive explanation, as Lickliter and Honeycutt implicitly propose, it would have no basis from which to predict the adaptive (or once adaptive) phenomena that EP currently attempts to explain. Contrastive explanations miss the general patterns described in comparative explanations, such as selective explanations. Even the richest account of how every individual in a population lived and died would leave an unbridgeable explanatory gap. Such causal life histories of individuals do not explain why they share traits, why some traits spread in populations, and why some disappear. In population-level evolutionary explanations these commonalities are identified as statistical properties of evolving populations, and statistical properties are appealed to only in comparative explanations. Any defensible evolutionary psychology would need to offer both kinds of explanation.

But would such a program be feasible? Would the combination of population-level analysis and DST result in 'population eco-devo-epi-genetics', a field perhaps doomed to failure by its own inclusiveness (but see Furrow et al. 2011)? This is not a necessary consequence. The population-level analysis could focus on the question, "Has the trait been selected for?", and the study of the epigenetic processes between and within generations could ask, "How does the trait develop?" and, "How is it inherited?" As Susan Oyama writes, speaking for developmental systems theorists, "Our emphasis on causal interdependence doesn't mean that everything is so connected to everything else that analysis is impossible, or that in order to study anything, you must study everything" (Oyama 2000, 344). Her endorsement of the tactical, provisional black-boxing of potentially important developmental resources can be extended to the tactical, provisional black-boxing of different biological questions and approaches. Some research programs are committed to answering both evolutionary 'why' questions and proximate 'how' questions. The phylogeny fallacy and the ontogeny fallacy arise when what should have been the temporary black-boxing of either kind of question has turned into permanent neglect.

Conclusion

I have argued that we should associate the phylogeny fallacy with the conflation of proximate and evolutionary explanation, rather than with Mayr's causal framework, with its use of the genetic program concept. This is in not to discredit Lickliter and Berry's arguments against this framework. I find their arguments compelling. From a DST perspective Mayr's framework is fundamentally flawed. However, those unconvinced by DST will not be convinced that a fallacy has been identified, as illustrated by the replies to Lickliter and Honeycutt's (2003a) target article. For the phylogeny fallacy to operate effectively as a regulative principle in the biological sciences it must point to a problem that is clear to those of all theoretical stripes. By removing its empirical premises and relocating the phylogeny fallacy to the conflation of proximate and evolutionary explanation I hope to have achieved this. As I have shown that this conflation of explanatory types must precede the problems identified by Lickliter and Berry, my solution should be germane to developmental systems theorists.

While the phylogeny fallacy, on my definition, is often a product of Mayr's formulation of the proximate/evolutionary distinction, Tinbergen's four-question framework may help us understand and avoid it. The fallacy is committed when the question of causation or the question of ontogeny is conflated with the question of evolution. Answering the questions of causation and ontogeny necessarily involves proximate analysis. An evolutionary theory inspired by functional analysis cannot answer the questions of causation and ontogeny because many causal and developmental pathways can potentially fill the same functional role. The problem with EP explanations in terms of genetic programs and mental modules is that they are often functional, rather than descriptive. They are theories about the evolved function of particular behaviours that are presented as proximate descriptions of the causes of those behaviours, when the causes are often not known. With regards to genetic programs, this is always true. With regards to mental modules, this is sometimes true, and must be judged on a case by case basis.

Lickliter and Honeycutt promote a new evolutionary psychology research program that abandons the distinction between proximate and evolutionary forms of explanation, focusing instead on the epigenetic processes of development within and between generations. I have argued (along with the respondents to the target article)

that this program could not displace EP. Whilst avoiding the phylogeny fallacy it would commit the inverse fallacy, the ontogeny fallacy. The ontogeny fallacy is less obviously fallacious than the phylogeny fallacy, yet the reasoning is simply inverted. Perhaps this is because, as Jackson and Pettit (1992) have observed, people tend to prefer fine-grained contrastive explanations to coarse-grained comparative explanations. We cannot use comparative information to explain fine-grained details. But can we use contrastive information to explain coarse-grained details? The answer is no, or at least not in the right way. Contrastive explanations are blind to comparative explanations, blind to patterns and their logic. Two people might have the same skin colour because they inherited similar developmental resources, but they also have the same skin colour because of a pattern of natural selection that is not grasped by fine-grained analysis. As I have argued, both kinds of explanation would have to be offered by a defensible, fallacy free evolutionary psychology.

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