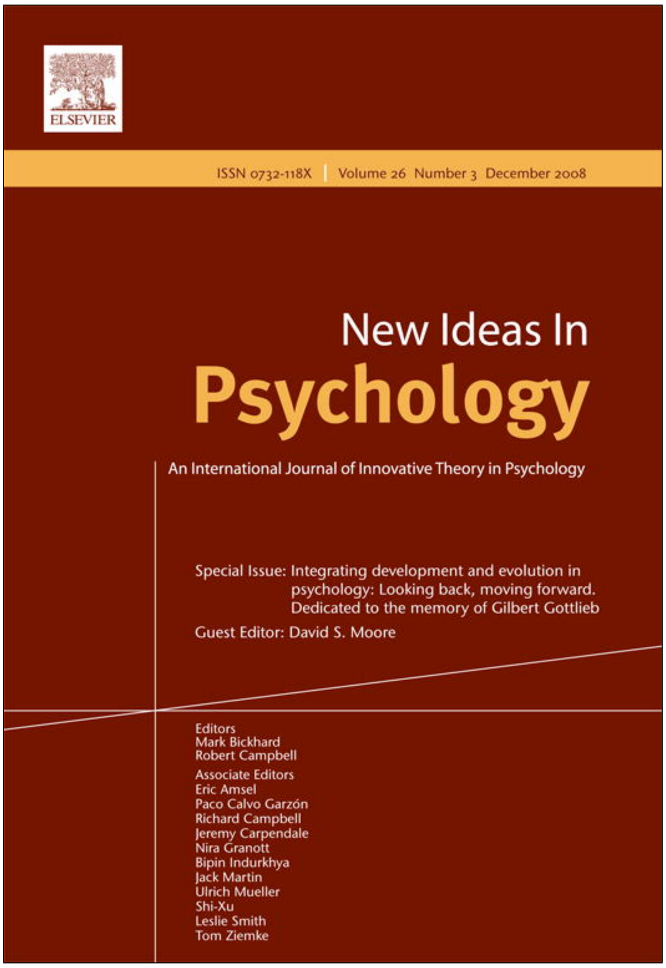
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Review

Taking old ideas seriously: Evolution, development, and human behavior

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Abstract

I argue that the roots of an adequate integration of evolution into psychology are not to be found in evolutionary psychology, but rather in evolutionary developmental biology (evo–devo). To this end, I provide an overview of evo–devo and explore the limited role that behavioral sciences have played in its genesis. I then motivate an evo–devo approach to psychobiology, and sketch desiderata for the success of this enterprise. In particular, I elucidate what it means to take both development and evolution seriously, and argue for the primacy of developmental analysis in the exploration of (human) behavior and its evolution.

Keywords: Developmental psychobiology; Developmental systems theory; Epigenesis; Evo–devo; Evolutionary psychology

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Contents

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1. Introduction

There are many ways to bring an evolutionary perspective to bear in psychology. These include the various strands of evolutionary psychology (EP), as well as efforts that fall within what I will call *evolutionary developmental psychobiology* (evo–devo psychobiology). EP begins with first principles, putatively borrowed from evolutionary biology (evolutionary *must be*'*s*), and applies these in attempting to explain the persistence and significance of contemporary behaviors. Evo–devo psychobiology, by contrast, begins with the putative facts of psychological development and behavior and our best understanding of their underlying mechanisms (developmental *actually is*'*s*), and then explores how these behaviors have evolved, how developmental mechanisms have evolved, and how behaviors and mechanisms may direct or bias future evolution. Within EP, evolutionary principles have pride of place, and evolution is the starting point of all analysis, such that evolutionary explanations constrain other forms of explanation. By contrast, within evo–devo psychobiology, development and evolution are both, severally and jointly, held high, but development is the starting point of all analysis, such that developmental explanations (or *sui generis* evolutionary developmental explanations) constrain other forms of explanation. My ambition in this article is to sketch evolutionary developmental psychobiology on an analogy with evolutionary developmental biology (Hall, 1999; Hall & Olson, 2003; Robert, 2004a), and to underscore its propriety at the heart of any adequate attempt to take evolution seriously in psychology.

2. Evolutionary psychology as a starting point?

Evolutionary developmental psychobiology does not exist as such. This article is intended as a positive contribution to the construction of an adequate theoretical framework for understanding the evolution and development of behavior and cognition, which I call evolutionary developmental psychobiology. I am not offering a full-blown critical inquiry of other such attempts, as within EP or behavior genetics (but see the other contributions in this issue, as well as Robert, 2005, for such efforts). Neither am I starting from scratch; others have attempted to bring evolution and development together in the domain of behavior and cognition (such as Lickliter & Honeycutt, 2003; Michel & Moore, 1995). But I am indeed attempting to discourage one particular genesis story for evolutionary developmental psychobiology, namely the 'developmentalization' of EP.

Some psychologists who study development (e.g., Lickliter & Honeycutt, 2003) have worried about the developmental implausibility of EP. They have underscored the necessity of developmental analysis for shedding light on the evolutionary history of behavioral traits, as against those within EP who seem not particularly worried about the developmental dimensions of their theories. Presumably, this is because evolutionary psychologists are engaged in 'population thinking' rather than in thinking about ontogeny at the level of individuals; or they may simply be preformationists and so see development as just the unfolding of what is predefined in the genes, or both (see Moore in this issue for more discussion).

But I think EP is simply the wrong starting point for evolutionary developmental psychobiology. Evo–devo psychobiology should not be just a developmentally plausible EP, in part because EP is not just developmentally implausible but also evolutionarily implausible—a point to which I return below. We must search further afield, beyond the bounds of psychology, for new and better sources of evo–devo psychobiology. Hence, the value of evolutionary developmental biology as a source of new ideas in psychology.

3. Exploring evolutionary developmental biology

Evolutionary developmental biology, affectionately known as 'evo–devo', is increasingly at the center of fascinating findings in biology today. Made wiser by a long history of prior and variously unsuccessful attempts to integrate developmental and evolutionary analysis, contemporary evo–devo borrows, co-opts, and integrates tools, techniques, and data sets from, *inter alia*, anatomy, cell biology, comparative genomics, developmental genetics, embryology, evolutionary biology, functional morphology, molecular biology, paleontology, physiology, and population genetics, in the service of discovering the ontogenetic, and evolutionary origins of form and function in all their diversity. Conspicuously, absent from this list is the behavioral sciences; with few exceptions (e.g., Gottlieb, 1997, 2003; cf. Robert, 2003), psychology and psychobiology have not informed contemporary evo–devo. (See Table 1 for a selective chronology of key publications and events in the genesis of present-day evolutionary developmental biology.)

Evolutionary developmental biology places developmental biology in an evolutionary context (including the evolution of development over time) and evolutionary biology in a developmental context (where evolutionary explanations are informed by the facts of development and of developmental possibility). Changes in development fuel the process of natural selection; the changes may be major—such as the fin–limb transition—or comparably minor—such as the evolution of specialized phenotypic markings. Even such apparently 'minor' changes may have a dramatic effect on survival, reproduction, and adaptive radiation. Evolutionary developmental biologists tend to contribute to one or more core projects. These include bringing developmental analysis, tools, and data to bear to solve evolutionary problems (such as integrating findings in development and morphology that disestablish the absolute presumption that all evolutionary change is gradual, e.g., Brylski & Hall, 1988a, b, discussed below); bringing evolutionary analysis, tools, and data to bear to solve developmental problems (such as using a phylogenetic perspective to guide the selection of animal models, e.g., Bolker, 1995; Jenner & Wills, 2007); and, eventually, perhaps, bringing developmental and evolutionary analysis, tools, and data to bear on *sui generis* problems properly within the domain of evolutionary developmental biology.

Table 1
Evolutionary developmental biology: a selective chronology of key events and publications

1958	Bonner's lectures on evolution and development at University College, London. These were published in Bonner (1958)
1961	Berrill's (1961) *Growth, Development, and Pattern*
1964	Davis's (1964) masterful monograph on the giant panda
1975	The German publication of Riedl's *Die Ordnung des Lebendigen*. (The English translation is Riedl, 1978.)
1977	Gould's (1977) *Ontogeny and Phylogeny*
1980	Hamburger's (1980) discussion of the exclusion of embryology from the modern synthesis
1981	Dahlem Conference; proceedings published as Bonner (1982)
1983	Raff and Kaufman's (1983) *Embryos, Genes, and Evolution*
1984	Arthur's (1984) *Mechanisms of Morphological Evolution*
1986	Wallace's (1986) critique, "Can embryologists contribute to an understanding of evolutionary mechanisms?"
1987	Buss's (1987) *The Evolution of Individuality*
1988	Arthur's (1988) *A Theory of the Evolution of Development*
	Thomson's (1988) *Morphogenesis and Evolution*
1990	A 'round-table discussion group' on the new field of development and evolution (involving 200 participants) at the *Fourth International Congress of Systematic and Evolutionary Biology*, proceedings published as Wake, Mabee, Hanken, and Wagner (1991)
1992	Hall's (1992) *Evolutionary Developmental Biology*, the first textbook of evolutionary developmental biology
1994	Rollo's (1994) *Phenotypes*: *Their Epigenetics, Ecology, and Evolution*
1996	Gilbert, Opitz, and Raff's (1996) call to 'resynthesize' evolutionary and developmental biology
	Raff's (1996) *The Shape of Life*, putting the emergence of morphological structures such as Bauplane at the center of the field
1997	Arthur's (1997) *Origin of Animal Body Plans*, continuing the exploration of Bauplan emergence advocated by Raff (1996)
	Gerhart and Kirschner's (1997) *Cells, Embryos, and Evolution*
	Niklas' (1997) *The Evolutionary Biology of Plants*
1998	Hall's (1998) *Evolutionary Developmental Biology*, much expanded second edition
	Schlichting and Pigliucci's (1998) *Phenotypic Evolution*: *A Reaction-Norm Perspective*
1999	Inception of *Evolution and Development and Journal of Experimental Zoology* (*Molecular and Developmental Evolution*) as specialist journals devoted to evo–devo
2000	Society for Integrative and Comparative Biology launches a new division, Evolutionary Developmental Biology, which holds its inaugural session; proceedings published in Burian, Gilbert, Mabee, and Swalla (2000)
	Arthur (2000) issues an evo–devo-based challenge to neo-Darwinism
2001	Carroll, Grenier, and Weatherbee's (2001) *From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design*
	Davidson's (2001) *Genomic Regulatory Systems: Development and Evolution*
	Wilkins' (2001) *The Evolution of Developmental Pathways*
	Dibner Institute Seminar in History of Biology, *From Embryology to Evo–Devo*, Marine Biological Laboratory, Woods Hole, MA
2002	Gould's (2002) *The Structure of Evolutionary Theory*
2003	Hall and Olson's (2003) edited anthology of *Keywords and Concepts in Evolutionary Developmental Biology*
	Minelli's (2003) *The Development of Animal Form: Ontogeny, Morphology, and Evolution*
	Müller and Newman's (2003) anthology, *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology*
	West-Eberhard's (2003) *Developmental Plasticity and Evolution*
2004	Arthur's (2004) *Biased Embryos and Evolution*
	Carroll et al.'s (2004) *From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design*, expanded second edition

Table 1 (*continued*)

	Robert's (2004a) *Embryology, Epigenesis, and Evolution: Taking Development Seriously*
	Schlosser and Wagner's (2004) anthology on *Modularity in Development and Evolution*
2005	Amundson's (2005) *The Changing Role of the Embryo in Evolutionary Thought*
	Burian's (2004) *The Epistemology of Development, Evolution, and Genetics*
	Publication of the first popular trade book on evo–devo, Carroll's *Endless Forms Most Beautiful*
	Kirschner and Gerhart's (2005) *The Plausibility of Life*
2006	Inception of *Biological Theory: Integrating Development, Evolution, and Cognition* as an interdisciplinary journal devoted to the study and theoretical elaboration of evo–devo
2007	Laubichler and Maienschein's (2007) edited collection, *From Embryology to Evo–Devo: a History of Developmental Evolution*

Adapted and updated from Table 1 in Sarkar and Robert (2003, p. 211) and Table 1 in Robert (2008).

Box 1
Evolutionary developmental biology: a selection of key problems.

- Determining relationships between phenotypes and genotypes (sometimes referred to as establishing the genotype-phenotype map).
- Understanding what explains the generation of variation and patterns of variation in nature.
- Explaining the role(s) of ecology (or more broadly: the environment) in shaping development and evolution.
- Studying major transitions in evolution and analyzing the developmental and phenotypic nature and appearance of evolutionary innovations.
- Unpacking the origin and evolution of embryonic and larval development and the nature and variety of such complex life cycles.
- Exploring the developmental basis of homology and expanding the prospects for successfully identifying homologies.

What it means to 'bring to bear' analytical tools or data sets is highly variable, and may involve importing new tools, posing new problems, conceiving old problems in a new way, reconceiving core concepts, newly identifying mechanisms or making them more salient, or simply contributing to explanations. See Box 1 for a selection of key problems within contemporary evo–devo. These problems (and others) are explored using comparative methods, experiments, and simulations. Sometimes, this work is conducted in single research programs, as in work by Brakefield et al. on butterfly wing morphology, which integrates tools and techniques from population genetics, evolutionary biology, ecology, developmental biology, and developmental genetics (e.g., Beldade, Brakefield, & Long, 2005; Brakefield & Kesbeke, 1997; Brakefield & Roskam, 2006; Roskam & Brakefield, 1999). More often, it seems that evo–devo research is conducted in interdisciplinary suites of programs across multiple labs whether formally linked together or brought into contact via review articles and conference symposia, and serving as fodder for new integrative hypotheses.

Examples of evo–devo in action help to flesh out its significance. The first example I will discuss is of how developmental analysis can shed light on evolutionary innovations, such as the evolution of furry cheek pouches in pocket gophers and kangaroo rats; the second shows how an evo–devo perspective adds new explanatory detail to a well-studied evolutionary phenomenon, changes in beak morphology in finches.[1]

Cheek pouches are useful during foraging for storage purposes. Rodents tend to have cheek pouches inside their mouths; these are lined with the same membranous tissue found in the rest of the mouth, buccal epithelium. But in geomyoid rodents such as pocket gophers and kangaroo rats, the cheek pouches are external to the mouth, and are lined instead (as you might expect) by fur. The external pouches tend to be bigger than internal ones, and they are more efficient in conserving body water than internal pouches. In now-classic experiments, Brian Hall's group at Dalhousie University showed that internal pouches are the ancestral condition and elucidated an evolutionary developmental account of the innovation of a fur-lined external pouch (Brylski & Hall, 1988a, b).

The key mechanism is epithelial evagination; evagination is when a body part turns inside out. In the ontogeny of the external cheek pouch, epithelial evagination begins at the corner of the developing mouth, which (uniquely in geomyoids) participates in the evagination; a small change in the location and magnitude of the evagination to include the lip epithelium at the corner of the mouth results in the production of the novel external pouch. As the lips grow in tandem with the snout, the evaginated corner of the mouth is transformed into the opening of the external pouch. Brylski and Hall showed that the external pouch was always furry as the ‘‘direct result of pouch externalization due to an inductive interaction resulting from the novel juxtaposition of the pouch and facial epithelia’’ (Brylski & Hall, 1988a, p. 394), rather than beginning as buccal epithelium and becoming furry over time.

No living geomyoids have both internal and external pouches; developmentally and functionally, it would be difficult to have both internal and external pouches. The developmental mechanism, epithelial evagination, is common. The developmental change is small, though the phenotypes are dramatically different. Together, these facts suggest that there is no intermediate ancestor between rodents with internal and rodents with external pouches. This means that changes in developmental mechanisms may produce coordinated change in an organism and provide the material and ontogenetic basis for new structures. Accordingly, as Garstang (1922) stipulated long ago, ontogeny creates phylogeny: evolutionary changes (whether microevolutionary or, as in this case, macroevolutionary) are driven by developmental changes (Fig. 1).

The second example I will discuss is variation in beak size in finches, specifically, Darwin's finches (genus Geospiza). Morphological variation in beak size is critically important in the survival and reproduction of populations of finches in the Galápagos Islands (Fig. 2). The finches' beaks are well adapted to climate-dependent food sources, including insects and seeds. Darwin's finches have long been seen as a rare example of ecologically driven ‘evolution in action' on a human, rather than a geological, timescale (Grant, 1986; Weiner, 1994). In a recent study (Abzhanov et al., 2004), scientists combined comparative and phylogenetic data with molecular data to analyze the developmental basis of these evolutionary changes (which were themselves initially revealed through natural history and ecological research). Bone morphogenetic protein 4 (*Bmp4*) is a member of a class of molecules involved in the onset of bone formation. These researchers showed that experimentally induced changes in the timing and location of *Bmp4* expression could

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[1] I have discussed the first example in Robert (2002, 2004a) and the second in Robert (2008); see also Carroll (2005) for an enthusiastic sampling of evo–devo research.

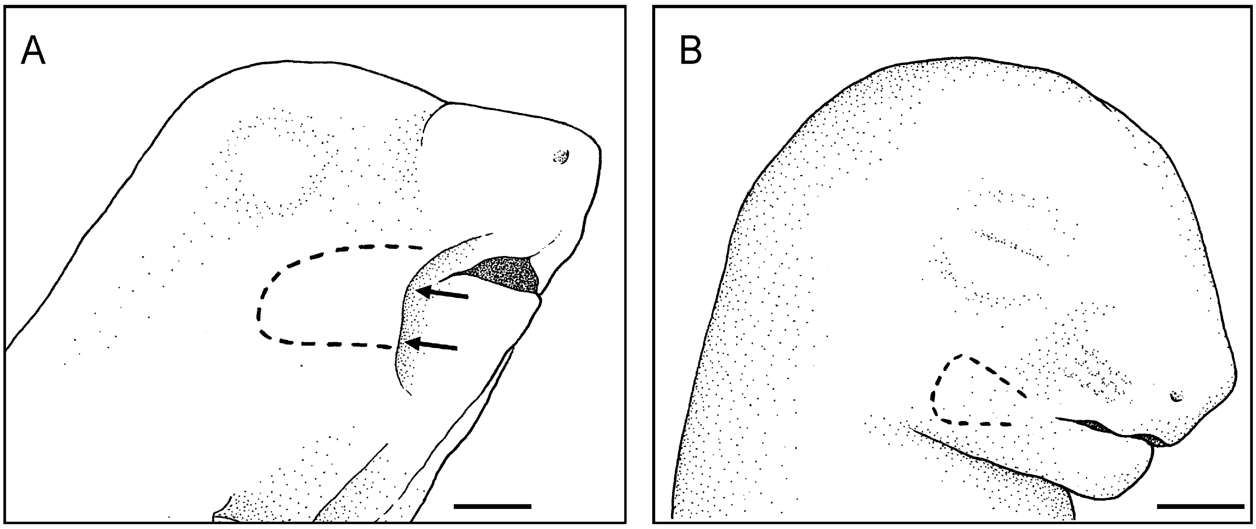

Fig. 1. External and internal cheek pouches. (A) Developing external cheek pouch in a neonatal *Dipodomys elephantinus* (big-eared kangaroo rat, approximately 30 days of age); arrows point to the anterior opening of the external pouch beside the mouth. (B) Internal cheek pouch in a prenatal *Eutamias minimus* (least chipmunk). Dotted lines trace the cheek pouches; scale bars = 2 mm. Reprinted from Fig. 11 in Robert (2004a), as redrawn and substantially modified by Tim Fedak from the photographs in Fig. 1 in Brylski and Hall (1988b).

account for the morphological differences between beaks in different species of the genus *Geospiza*. As one commentator has noted, "these findings elucidate the developmental origin of an adaptive radiation that serves as the textbook example of evolution" (Sinervo, 2005, p. 101). Even though the evolutionary story about *Bmp4* remains to be fully fleshed out, these results exemplify the integrative potential of evo–devo even for well-studied cases of evolutionary interest.

4. Motivating evolutionary developmental psychobiology

Though the behavioral sciences have not been at the core of contemporary evo–devo, there is no good substantive reason for this to have been the case. I suspect that this absence is the result of two interesting accidents: on the one hand, EP arose outside the mainstream of evolutionary biology (Lloyd & Feldman, 2002) and has always been devoid of any developmental sense (as explored by Lickliter & Honeycutt, 2003, and in the papers in this issue by Lickliter and Moore); on the other hand, the field of evo–devo historically focused on the embryogenesis and anatomy of form (see, e.g., Love, 2003). But EP is severely limited in outlook and is methodologically fraught (as shown by Buller, 2005; Francis, 2004; Lloyd, 1999; Lloyd & Feldman, 2002; Ratcliffe, 2005, *inter alia*; cf. Downes, 2001), and the contemporary agenda of evo–devo is broadening quite dramatically (e.g., as evidenced by the breadth of the chapters in Hall & Olson, 2003). As a result, the future for a new evolutionary developmental psychobiology is bright.

It is, of course, not novel to envision and call for the integration of evolutionary and developmental analysis in psychology. These are not new ideas. Gilbert Gottlieb and others seeded one strand of this project four decades ago. Consider Gottlieb's early experiments that challenged the ethological innate/acquired distinction.[2] Gottlieb asked,

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[2] My discussion of this research draws on Robert (2008).

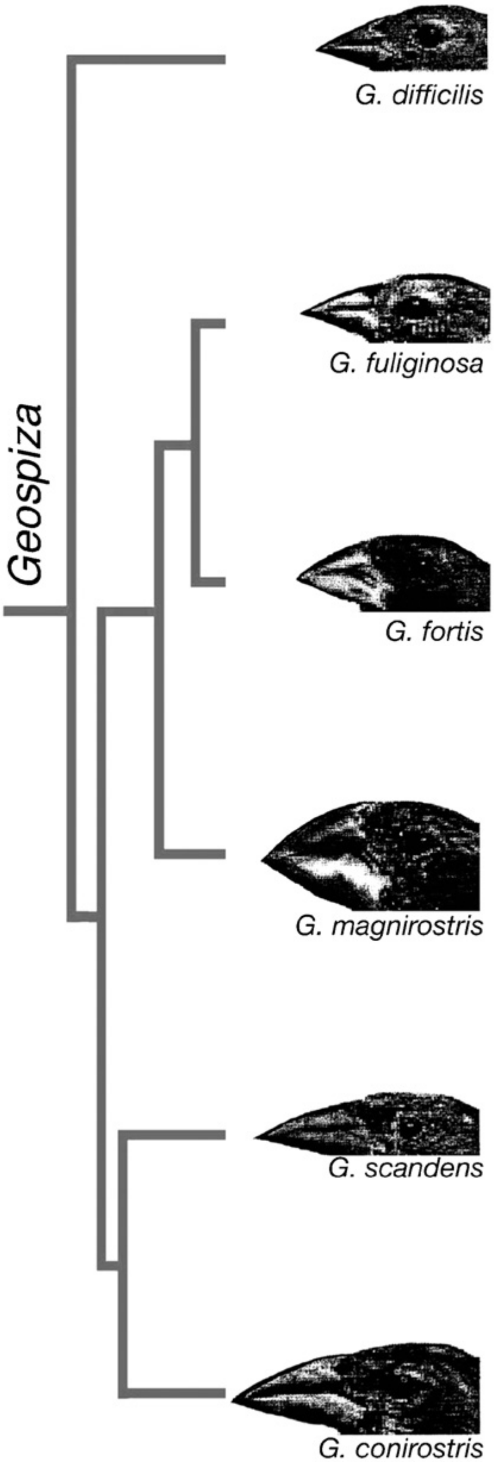

Fig. 2. Finches of the genus *Geospiza*, exhibiting characteristic variation in beak morphology and size. Reproduced from Figure 1a in Abzhanov, Protas, Grant, Grant, and Tabin (2004).

what explains the ability of newborn duck hatchlings to recognize and respond to their species-specific maternal call? Two responses to this question were (and, unfortunately, remain) standard fare: either the ducks are developmentally 'pre-programmed' to act in this way and so inherit this capacity, or they acquire this facility shortly after birth as a result of experience. Gottlieb designed and conducted many experiments to test these alternatives, and concluded that the explanation was more complex than either one. His devocalization experiments on mallard ducklings were part of his effort to understand whether *prenatal experience* facilitates the development of the new hatchlings' species-typical preference for the species-specific maternal call (see Gottlieb, 1997, for his own account of these early experiments).

Gottlieb gave mallard hatchlings an opportunity to choose to approach one or the other of two speakers broadcasting different calls, to demonstrate their selective preference for their species-specific maternal call. He found that the hatchlings unfailingly recognized their own species-specific maternal call, approaching the speaker broadcasting that call and not the other speaker broadcasting the call of a different species. Though this result is compatible with either alternative, it is usually taken to support the claim that the behavior is inherited. But Gottlieb had another idea. He hypothesized that *prenatal* experience (not genetic inheritance, not postnatal learning) might play a role in facilitating the behavior. Part of his motivation was that the ducklings begin vocalizing shortly after they begin to breathe—as embryos, several days prior to hatching. So he developed a surgical technique for temporarily devocalizing the ducklings *in the egg*. The experimental surgery required using Chinese writing brushes to apply a non-toxic surgical glue (Collodion) to the vibratory membranes of the embryonic voice box; this glue temporarily rendered the embryos mute, though they were able to vocalize again after several weeks. The control groups were permitted to vocalize for some hours before either being surgically devocalized in the egg, or undergoing a 'sham' surgery.

Gottlieb's findings were significant. He found that at 24-h post-hatching, the devocalized embryos, forbidden from self-stimulation and sib simulation (the sibs were similarly devocalized), had less facility in distinguishing the mallard maternal call from the chicken maternal call. By contrast, the control hatchlings had no such difficulty. Together, these results indicate a facilitative effect of embryonic auditory experience on the development of auditory perceptual skill. At 48-h post-hatching, the difficulty is apparently rectified. But at 65-h post-hatching, the devocalized hatchlings are again deficient. These latter results indicate a maintenance effect of prenatal exposure to self- and sib vocalizations—else the 65-h-old devocalized hatchlings would have retained the capacity they had at 48 h to distinguish the mallard maternal call.

What makes these results all the more interesting is that the prenatal vocalizations of embryonic ducklings are acoustically quite different from the maternal species-specific call, so it is not as if hearing their own voices provides embryos access to their maternal species-specific call. Accordingly, it appears that a particular prenatal experience stimulates (facilitates) the development of the embryo's auditory system so as to lead it to selectively prefer its own species-specific maternal call, even though that call is quite different from its own and its sibs' vocalizations. Postnatal preferences therefore depend in some ways (at least quantitatively) on prenatal experiences of a different character. From an evo–devo psychobiological perspective, the upshot is that the details of behavioral development are important to understanding transgenerational stability of form, which is of course the basis of heredity and so of evolution.

Gottlieb was an invited contributor to Hall and Olson's important anthology on *Keywords and Concepts in Evolutionary Developmental Biology* (Gottlieb, 2003; Hall & Olson, 2003). In inviting his essay, the editors clearly recognized the value of Gottlieb's scientific efforts for evo–devo, and so also recognized the potential for the behavioral sciences to contribute to the further elaboration of the field. But I think it is also clear that in addition to offering a psychobiological perspective within evo–devo, Gottlieb's work is exemplary of an evo–devo approach within psychobiology. What, then, are the determinants of an evolutionary developmental psychobiology adequate to the task of explaining the development and evolution of behavior, including human behavior? I discuss two key ingredients: taking development seriously, and taking evolution seriously. No current theoretical framework does both, and some (e.g., EP) do not do either.

5. Taking development seriously

To take development seriously requires understanding that (a) there is more to development than differential gene expression (which is only part of the story), (b) that development is not a genes-*plus* (environment, stressor, trigger) phenomenon, and (c) that the causal analysis of development (epigenetics) is required to understand evolution.

5.1. There is more to development than differential gene expression

In the hands of some commentators (e.g., Rosenberg, 1997; Schwartz, 1999), and even some biologists (e.g., Carroll, Grenier, & Weatherbee, 2004; Gehring, 1998), the logic of differential gene expression is mistaken for the logic (and, indeed, the process) of development. The differential expression of genetic elements in particular tissues at particular moments is surely part of any account of development, absolutely. But there is much more to development than gene expression. For instance, development begins *prior* to gene expression (physico-chemical factors are at work in cell division long before genes contribute to developmental processes). Moreover, many aspects of development occur independent of or despite gene activity (such as autonomous human behaviors with developmental consequences mediated by the brain but not necessarily by the genome in any specific way). And developmental processes are often robust in the face of errors in gene expression (which is why everyday transcription errors only occasionally result in developmental mayhem). Accordingly, to mistake differential gene expression for development is to mistake a part for the whole. Confusion abounds. Consider John Maynard Smith's accurate contention that there is "a lot more to development than gene regulation" alongside his fraught claim, in the very next sentence, that, "in particular, there is the question of how genes get switched on in the right places" (Maynard Smith, 2000b, pp. 217–218). Presumably, he is contending that the positional aspects of gene regulation are as important as the timing of gene regulation; but these are merely two sides of the gene expression coin—not the piggy bank that comprises development as such. But classes of non-genetic developmental causes that both interact with and operate relatively independently of the genome have been long recognized, if commonly ignored (see, e.g., Moore, 2002; Oyama, Griffiths, & Gray, 2001; Robert, 2004a; van der Weele, 1999).

5.2. Development is not a genes-plus phenomenon

Those who agree that development is not *exclusively* a genetic affair might still pretend that development is *primarily* a genetic affair. This idea that genes are *first among equals* (Schaffner, 1998) has motivated some biologists and commentators (e.g., Maynard Smith, 2000a, b; Rosenberg, 1997) to hold that development reduces to genes-*plus* chemical or other environmental signals that trigger the potential residing in the genome. The metaphor of triggering is, so to speak, a loaded one; is it the right one for development? To trigger is to set in motion a (pre-arranged) sequence of events, such that the eventual outcome can be traced back to that initiating event—as in pulling a trigger on a gun, or pulling a pin on a grenade. When the trigger is pulled, the sear releases the firing pin, which in turn leaps forward to strike the primer. A jet of flame from the primer ignites the powder, forming a gas. This explosive gas propels the bullet from the barrel. But the gun analogy is obviously misplaced here, as organisms are considerably more complex and less predetermined than firearms. To buy this analogy, one must believe that everything necessary for the specific transformations that occur during development is right there in the embryo, lined up in close proximity like the parts of a gun, ready to act when acted upon. Preformationism of this sort has no place in contemporary biology, as development clearly involves the epigenetic emergence of complexity over time (Robert, 2004a).

Triggering is an additive notion: gene-*plus* environmental or chemical stressor, program *plus* command execution, the unleashing of potential always already there in the genome. Yet, to paraphrase Gray (1992) on developmental information, whatever developmental potential there is resides not *in* genes or *in* other developmental resources but rather emerges *from* their synergistic *interaction*. This is a nonadditive account of interaction, one far more in line with the facts of biology than the triggering metaphor ever was (Robert, 2004a).

5.3. *Studying epigenetics is essential to understanding evolution*

The discussion in this section so far suggests the need for a sustained focus on the causal analysis of development—C.H. Waddington's early definition of 'epigenetics' (Waddington, 1952). The developmental biology that most adequately informs evo–devo is modestly reductionistic and gene friendly (though non-gene-centric). It explores how development actually happens—the dynamics of development. Rather than invoking metaphors, experimentalists manipulate a range of developmental factors (such as DNA, histone and non-histone proteins, enzymes, hormones, metabolites, and parental effects) that interact to produce the phenotypes that comprise organisms; in the case of humans, this includes our remarkable bodies and the complex architecture of our brains and their behavioral and cognitive products.

Evo–devo takes the study of how development actually occurs as the basis for exploring, amongst other phenomena, how development serves to influence evolutionary change through the generation of 'biased' or constrained variation. Insofar as the range of evolutionary possibility is shaped by developmental possibility and actuality, the study of epigenetics matters crucially to the study of evolution, behavioral and otherwise.

By contrast, within EP, "the idea that all of biology and psychology can be explained by past events of differential reproduction and selection continues to hold strong" (Lickliter & Honeycutt, 2003, p. 826). Accordingly, to evolutionary psychologists, 'proximate' explanation (development) matters considerably less than 'ultimate' explanation (evolution, putatively). This particular bias manifests in *evolutionary must be*'*s* trumping *developmental actually is*'*s*. The presupposition that such and such *must be* a certain way because of how natural selection optimizes phenotypes (or some such putative evolutionary first principle) often effectively ignores what we know to *actually be* the case developmentally.

6. Taking evolution seriously

Evolution is an historical science; it must not be about *must be*'*s*, but rather about the contingent ecological interactions (and other mechanisms), within and between entities, that cause differential survival and reproduction. To take evolution *really* seriously is to test developmental hypotheses within phylogenetic frameworks, and to try to integrate the results of developmental analyses with the data of population geneticists and with well-validated models of evolutionary change. But to take evolution seriously enough for our purposes is, at least, (d) to understand that organisms develop and evolve in complex ecological contexts, (e) that interactions between organisms, and between organisms and environments, can be important in elucidating particular developmental and evolutionary trajectories (and vice versa), and (f) that to recognize variation within and between species is important for avoiding bad generalizations.

6.1. Organisms exist in complex ecological contexts

This point requires no unpacking, except to say that these complex ecological contexts are not somehow independent of the organisms that inhabit them. And vice versa, because the organism's development does not proceed independently of the environment. Indeed, the co-construction of organism and environment is increasingly widely accepted, whether through the explanatory mechanism of niche construction (Odling-Smee, Laland, & Feldman, 2003) or by other means (Lewontin, 2000; Robert, 2004a). This co-construction has dramatic evolutionary effects, effects that may be misunderstood unless we take development seriously.

6.2. Ecological interactions can elucidate developmental trajectories—and vice versa

Similarly, this point requires very little unpacking. The evo–devo story about Darwin's finches illustrates the basic idea, given the integration of natural history with developmental genetic and ecological analysis. Consider also the full range of environmental causes of particular phenotypes, such as temperature-dependent sex determination in turtles, population-density-dependent sex determination in roundworms, host-dependent phenotype development in parasitic wasps, and predator-induced polyphenism in water fleas (as discussed in Robert, 2004a; van der Weele, 1999). The latter is an exceptionally clear example: the morphology of *Daphnia* will be altered if the juvenile fleas develop in water in which their predators have been reared, even if the predators are no longer present (Gilbert, 2001). This is an instance of ecological induction: the predators release chemicals to which the fleas have evolved a morphological response—a helmet. The helmet permits easier escape from the predator, and so the morph benefits from the ecological induction, even though the helmet may come at a cost—it may limit resources for provisioning eggs—exemplifying a developmental/evolutionary trade-off (Gilbert, 2001). Understanding ecological interactions—whether between organisms of the same or different species or between organisms and other elements of an environment—sheds important light on the nature of developmental processes and organismal 'lifelines' (Rose, 1997), which in turn helps to explain the range of evolutionary possibility.

6.3. *Recognizing variation within and between species helps to avoid bad generalizations*

Taking evolution seriously within developmental biology forces a comparative perspective that is otherwise all too uncommon for developmentalists. In developmental biology, generally (as elsewhere, e.g., Saikkonen, Lehtonen, Helander, Koricheva, & Faeth, 2006), the use of a small number of model organisms has generated conceptual and philosophical debate specifically related to the drawing of inferences from model organism-based research. "It is widely recognized both that model organisms are essential to research, and also that, in part because model organisms are highly derived research tools, research based on them may not always be appropriate sources of scientific inference; that is, models may not always serve as appropriate proxies" (Robert, 2004b, p. 1008).

One standard justification for experimental study with model organisms (such as mouse, frog, nematode worm, or chick) is that model organisms are experimentally tractable: they yield to analysis. They tend to be developmentally simple (Schaffner, 1998), and they are specifically made to be analyzed (Gilbert & Jorgensen, 1998; Kohler, 1994; Rader, 2004). "Model organisms are both selected and selectively fashioned in order to make experiments work, and use of the same material by different scientists facilitates replication (or disconfirmation) of results" (Robert, 2004b, p. 1008). Experimental research with such models has been very productive in some domains (see Shultz, Ishikawa, & Greiner, 2007, on humanized mice, for instance; see also Bier & McGinnis, 2004 for a more general review). But there are distinct and pronounced liabilities associated with research based on such models (Ankeny, 2000, 2001; Bolker, 1995; Bolker & Raff, 1997; Creager, 2001; Gilbert, 2001; Gilbert & Jorgensen, 1998; Gottlieb & Lickliter, 2004; Rader, 2004; Robert, 2004a, b; Saikkonen et al., 2006; cf. Weber, 2004), such that any scientific inference on the basis of model organism research must be cautiously drawn.

An obvious antidote is to emphasize the value of rigorous interspecific comparative research:

> Neuroscientists make inferences about the human brain by studying nonhuman species, an enterprise that depends on assumptions about the nature of evolution. Traditionally, many neuroscientists have supposed that all mammals possess variants of the same brain which differ only in size and degree of elaboration. Under this model, the brains of nonhuman species can be treated as simplified versions or models of the human brain. However, there is evidence that mammalian brain organization implies that neuroscientists can make better inferences about human brain organization by comparing multiple species chosen [on the basis of] their evolutionary relationships to humans, [rather] than by studying individual 'model' or 'representative' species. The existence of neural diversity also suggests that nonhuman species have evolved cognitive specializations that are absent in humans. (Preuss, 1995, p. 1227; see also Preuss, 2000)

Moreover, it is important to recognize the limits of comparisons, especially in the context of behavior, and especially in the case of humans (Povinelli, 2004, is especially good on this point). As Gottlieb and Lickliter underscore, "it is actually dubious that nonhuman primates can serve as models for the most distinctive of human cognitive abilities, any more than we could serve as good models for their distinctive traits" (Gottlieb and Lickliter, 2004, p. 317). Yet this recommendation for rigorous comparative research has been resisted for pragmatic or ethical reasons, however poorly justified.

7. Conclusion

On the basis of the preceding discussion, and as I hinted at the outset, one modest suggestion is that evolutionary psychologists fail to take evolution seriously, so construed, just as they fail to take development seriously. (For arguments to this effect, rather than just a simple restatement, see Buller, 2005; Lickliter & Honeycutt, 2003; Lloyd & Feldman, 2002; Quartz, 2003, and the articles by Moore and Lickliter in this issue.) As Lickliter and Honeycutt remark, "If evolutionary psychology's aim is to understand the evolved psychological mechanisms that underlie behavior and the selective forces that have shaped these mechanisms …, then it seems to us that uncovering the network of factors (both internal and external to the organism) that bring about and maintain (or eliminate) transgenerational similarities or differences in behavioral traits should be a prominent goal of EP" (Lickliter & Honeycutt, 2003, p. 829). Accordingly, EP is an inappropriate starting point for an adequate developmental evolutionary psychobiology. A more fruitful starting point is evolutionary developmental biology,[3] where standard practice is to refuse *must be*'*s* in favor of *actually is*'*s*, and to take both evolution and development with due seriousness.

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[3] Though I cannot elaborate here, I have elsewhere underscored the importance of a critical ongoing conversation between evolutionary developmental biologists and developmental systems theorists (Oyama, 2000; Oyama et al., 2001) so as to liberalize the account of evolution and moderate the inordinate gene-centrism of some evo–devoists. See Robert, Hall, and Olson (2001) and Robert (2003, 2004a).

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