Developmental Science 10:1 (2007), pp 30–34 DOI: 10.1111/j.1467-7687.2007.00560.x

Endless minds most beautiful

Barbara L. Finlay

Department of Psychology, Cornell University, USA

Abstract

The marriage of evolution and development to produce the new discipline 'evo-devo' in biology is situated in the general history of evolutionary biology, and its significance for developmental cognitive science is discussed. The discovery and description of the highly conserved, robust and 'evolvable' mechanisms that organize the vertebrate body plan and fundamental physiology have direct implications for what we should investigate in the evolution of behavior and cognition.

> There is a grandeur in this view of life . . . from so simple a beginning, endless forms most beautiful and most wonderful have been, and are being, evolved. (Charles Darwin, *The origin of species*, 1859)

Evolution itself evolves, as evolving organisms come to carry the history of successful solutions to the recurring challenges of life on earth in their genomes and in their epigenetic expectations of the structures the environment will support and inform. Our understanding of evolution has also evolved, very rapidly of late. The title of this essay is a double-reference, not only to the often-quoted last sentence of *The origin of species* but also to Carrol's recent book *Endless forms most beautiful: the new science of evo devo* (2005), one exemplar of a current outpouring of both scholarly and popular works on the unexpected wealth of understanding that has arisen about the current structure of organisms, their development, and their evolution when the three domains are closely compared (just a few: Wilkins, 2001; Gould, 2002; West-Eberhard, 2003; Kirschner & Gerhart, 2005). 'Evo-devo' as a discipline so far has primarily concerned itself with the evolution of fundamental body form, physiological processes and their genomic specification in basic vertebrate and invertebrate radiations, with some consideration as to types of mechanisms that emerge when nervous systems elaborate themselves.

This essay will have two parts, the first a bit of didactic scolding about the necessity for developmental scientists to keep themselves informed of progress in evolutionary biology, including a brief outline of the history of evolutionary biology. The second part is an exhortation to begin including this new view of evolution into developmental science, with some specific suggestions. I will contend that a good majority of psychologists, cognitive scientists, biomedical researchers, and even biologists do not understand the implications of current work in the evolution of development and employ instead an outmoded gene/environment conceptual scheme that ill suits what we now know is out there. I will borrow from Gerhart and Kirschner's several expositions of the kinds of organization in organisms that are 'evolvable' (1997, 2005) and suggest how their concepts might be imported into developmental science.

A very brief history of evolution

Darwin's *Origin of species* and subsequent works concerned themselves with the historical relationships of current species, with the insight of natural selection and sexual selection: that natural variations in organisms' ability to survive, find mates and reproduce, if heritable, inevitably produce evolution in the traits animals possessed. This argument was based on the reasonable assumption of selection on a distribution of small random variations, accumulating over long evolutionary time, which could produce anything from quantitative variation in morphology – for example, beak length – to a novel complex organ – for example, an eye. Darwin knew little of the quantitative aspects of heritability and nothing about the actual genetic mechanisms that preserve information about a particular organism's attributes over generations.

The 'Modern Synthesis', germinating with Mendel, to Watson and Crick, to the current vast number of individuals working on transcribing the genome, synthesizes the Darwinian view of adaptation, selection and evolution with its mechanism – the particular features that DNA

Address for correspondence: Barbara L. Finlay, Department of Psychology, Cornell University, Ithaca, NY 14853, USA; e-mail: blf2@cornell.edu

as a molecule confers on the process of evolutionary change. Just how genes replicate, the kinds of errors made in this process, how genes are transcribed to proteins, and how proteins typically build cells confers an enormous amount of structure onto the kinds of organisms that are possible, and changes permissible. Within this context, variations observed are assumed to be essentially random. In the modern synthesis, as described most eloquently by Dawkins (1976), the fundamental component of evolution becomes the gene, the digitally self-replicating unit that clothes itself in a phenotype and whose success is measured in its replications. The unit of evolution is not the individual organism and most assuredly not the species. At a mechanistic level, the operation done by a gene was thought to be explicit: each gene codes a protein (but see Pearson, 2006). These proteins in turn may have diverse functions: they could control what other parts of the genome are expressed and how long by altering the packaging and transcription of the DNA molecule; as enzymes or components of enzymes they could chaperone the construction of diverse types of structural or signaling molecules; or they could become parts of the organism's signaling or structural components directly, for example, as a neurotransmitter or a component of muscle.

Dawkins particularly has been at pains to defend the essential tenet of gradualism in Darwin's view: that any structure, no matter how complex and precise, can be built up in small increments by selection from random variation, with each new stage adaptive compared to its predecessor. For structures built *de novo* this must certainly be true, and the modeling of these processes is quite persuasive. The eye, an organ Darwin was puzzled to explain, can be built in enumerated steps, each a little better than the one before, i.e. an eyespot to register light; protection of the eyespot; several units amid the spot to confer directionality and so forth. In fact, across phyla every diverse kind of 'intermediate' eye can be found, though of course the point is that no particular eye in an existing animal is on its way toward a goal of greater complexity or better design and each eye is satisfactory for its particular niche (Land & Nilsson, 2001; Fernald, 2004).

The first mechanistic account of how genes work, necessarily oversimplified in its beginnings, coupled with the idea that every component of an organism is adaptive with respect to its immediate, or immediately historical, environment produced gigantic research initiatives, which have produced both remarkable successes and remarkable failures. The first enterprise is to locate 'the gene for X' where X might be a single structural or signaling protein, like an opsin, or a membrane receptor (or their disorders, color blindness or muscular dystrophy, for example), or a trait of extreme complexity with respect to a single protein, like reading or intelligence (or their disorders, dyslexia or retardation). Of course, no sensible researcher would presume a single gene for every nameable trait, and the rapid invention of technology of immense complexity for identifying multiple genes that contribute to smaller and smaller amounts of the variation in complex traits is surely one of the major achievements of current genomic work. However, even for simple traits, considering that genes are duplicated and redundantly represented in multiple body components, often with radically different functional roles in their separate sites, and that the effect of a gene may be the control of the duration or amount of expression of another gene at a particular point in development, that expression dependent on the immediate environmental context (these features of the genome to be discussed more later), it is remarkable that this approach ever works. Keller and Miller (2006) have an excellent review of the conceptual and empirical literature of the genetics of mental disorders that illuminate the implicit models we bring to the genetics of complex traits.

A second enterprise related to the explicit gene mechanism/universal adaptation view is the current reincarnation of the just-so story in the field of evolutionary psychology (Barkow, Toobey & Cosmides, 1995). Some just-so stories are in fact just-so, and the attempt to find the evolutionary roots of human behavior is entirely laudable, though the Pleistocene may not be far enough to excavate. However, there are some odd mistakes in logic that crop up repeatedly in explanation of human behavior, which I will expand on a bit before returning to the present stage in the account of the evolution of evolution.

Sources of predictability and universality

One maddening habit of the popular press, many introductory textbooks, and a large percentage of social scientists at any university is to contrast 'biological' and 'cultural', where 'biological' implies predictable, universal, rule-based and genetic, and 'cultural' variable, undefined and plastic. In fact, universality is often taken as explicit evidence of the genetic determination of some behavior or cultural pattern (for example, Buss & Schmitt, 1993). The secondary assignment of a political stance to preference for one or the other class of explanation is more maddening still. It just isn't so. The reader is referred to Jablonka and Lamb's *Evolution in four dimensions* (2005), an entertaining account of how genetic, epigenetic, behavioral and cultural transmission of information can each produce complete predictability or variability in simple or complex traits of interest, from which these examples are generally drawn. For example, all the cells in any individual's liver

are genetically identical to the cells in the same individual's brain, yet in each organ its stem cells reliably produce only cells of the appropriate type, this controlled by epigenetic factors (of either ultimate 'environmental' or 'genetic' origin) which control which genes will be expressed and what environmental information sampled. In the behavioral realm, consider the identical genomes of queen, worker and nurse bees, induced by each individual's environmental history to produce diverse behavioral capacities. Jablonka and Lamb describe and populate an alternative planet with as diverse species as earth's, whose genomes are identical to each other and whose diversity is produced entirely by known epigenetic mechanisms, and is heritable – i.e. transferred from one generation to the next, but with the same underlying DNA.

In contrast to the usual argument, the environment can be an extreme source of stability for nervous systems and behavior. For all of the history of life on earth, the sun has risen and set each day, and the genome takes in this information to set its internal clocks (Fernald, 2004). The stability of the statistics of the visual world and what sort of data reduction best expresses its structure in combination build visual systems of completely interleaved genetic and learned structure (Field, 1994). The more so when animals must inhabit a particular kind of niche – if it is required that you have parents to survive, only crude mechanisms need orient you to the parent, and general learning mechanisms can take it from there, building species-specific preferences for free (Johnson & Morton, 1991). Basic statistical learning can extract from the necessary parental environment basic regularities of language; operant learning the sexiest way to sing or talk (Goldstein, King & West, 2003). Cultures learn what food supports you and what poisons you, and what a group ingests may stay stable for centuries without any individual ever exploring the limits of the edible in their environment.

There is a lot of hard work to be done tracing the sources of stable information structures through the genome, and through epigenesis, individual and cultural learning. Understanding of language, emotional communication, the elaboration of the concept of agency and theory of mind, the development of behavioral control are all current topics that would benefit from the evo-devo frameworks to be described. Finally, it would also do well to remember that there is nothing particularly liberal about the environment that contrasts with the conservatism of the genome.

Unexpected developmental structure in evolution

My colleagues and I have extended this account in several earlier papers (Finlay, 2005; Finlay, Cheung & Darlington, 2005). This section is a précis of the empirical and interpretational changes that began in the early 1990s when it became possible to identify regulatory genes and the proteins that are expressed in early development across phyla. The attention-getting demonstration for many was the experiment that a regulatory gene, Pax-6, which in a mouse or human directs the organization of an eye in its domain of expression, if inserted into a *Drosophila* embryo, directs the expression of a *Drosophila*-specific compound eye where it is placed (Callaerts, Halder & Gehring, 1997). Subsequently, extensive conservation of the regulatory genes that direct the polarity and segmental organization of the vertebrate and invertebrate body plan was demonstrated, as well as the conservation of particular developmental mechanisms – in the case of the brain, for example, the molecules directing axon extension and halting, or synaptic stabilization through calcium signaling. This conservation of developmental mechanisms served to back-illuminate the conservation of a wide number of fundamental cellular processes. Because it is commonplace to do so, for example, researchers don't often view it as a remarkable fact that it is possible to use the marine mollusk *Aplysia*, pigeons and rats all as 'animal models' for learning, both at the level of cellular mechanisms and at the level of their organismal responses to various classes of reward regimes (Greenough & Bailey, 1988).

Why this conservation? The general answer is that while evolution can fit each creature into an adaptive niche by successive small steps, all life on earth has also been repeatedly filtered through local and global catastrophes for those developmental and physiological mechanisms that are robust and stable to environmental challenges, that are by definition 'evolvable'. A version of the modern synthesis, integrating the properties of DNA itself into evolutionary history, comes in as well: the propensity of the genome to evolve by the general tactic of duplicating (or multiplying) itself at the level of the single gene, chunks of genes or the whole genome. This tactic has the advantage of conserving basic organismal mechanisms while allowing local temporal or spatial variations in the duplicated gene, and allows access to old adaptations in a way a single, constantly overwritten set of genes could not. Gerhart and Kirschner, in their two books *Cells, embryos and evolution* (1997) and *The plausibility of life: Resolving Darwin's dilemma* (2005), have begun to analyze the organizational properties of conserved and evolvable developmental systems. To conclude, I will briefly recount the properties they have proposed and argue that we should export them wholesale as a way of examining brain structure and cognition, because the requirements of appreciating and moving in the environment, predicting the future, finding mates and raising

young are fully as ancient as the body plan, and should benefit from the same explanatory scheme.

Four properties of evolved and evolvable systems

The features Gerhart and Kirschner observe are the following. First, fundamental 'physiological' processes are conserved. In the case of cell biology, they are referring to such processes as oxidative metabolism, the transcription of genes and construction of proteins, and basic signaling systems between extracellular and intracellular space. I have already mentioned the associative learning demonstrated by *Aplysia*, rats and humans as one example of a conserved 'physiological mechanism' shown by (arguably) all nervous systems we have investigated. We should attempt to expand this category to look for similar basic solutions to data reduction and representation systems, motor control systems and homeostasis. In addition, it is quite possible that any nervous system needs a fundamental repertoire of distinct learning mechanisms. To list a few candidates for such a list, consider these processes characterizing large mammalian brain systems: associative learning with different time constants; error-driven learning, as in the cerebellum; learning by reinforcement (Atallah, Frank & O'Reilly, 2004), and learning through prediction (Elman, 1990). It would be interesting to re-examine development with an eye to how fundamental operations like these are first deployed and integrated.

Second, they argue for modularization of function, as is seen so repeatedly in the segmentation of the body plan and also in the nervous system. It is important to note here that the word 'module' is used in a different way in biology than it is in cognitive science. Segmentation is a common embryological feature that is closely related to the 'duplicate and vary' genomic strategy previously described, and allows initially identical structures to diverge in function, for example, as in spinal cord segments innervating the leg versus the body wall. Since the same genes are being deployed in each segment, in order to produce variation, local modifications of genetic cascades must be protected from constraining effects of pleiotropy. To take a familiar example to cognitive scientists, while the gene 'Fox P2' may be linked in several taxa to improvements in rapid vocal behavior (Teramitsu, Kudo, London, Geschwind & White, 2004), but is expressed widely in the developing organism, and to change the amount of its expression in every location it is expressed could not possibly be a benefit. The brain presents us with a diversity of potential modular structures in this sense, from the segments of the spinal cord, the rhombomeres and prosomeres that are the initial segments of the brain, the cerebellum and the repeating columns of all the cortical structures of the forebrain, hippocampus, neocortex and olfactory cortex. Of course, one of the most central and persistent arguments in cognitive science is whether there is modularity in language at the functional level and whether this modularity has a direct mapping onto brain parts. I would suggest that we have become mired in the discussion of this particular case, and should step back and return to the biological 'theme and variation' version of modularity and whether it might have application to cognition more generally. For example, some region of the cortex might become specialized in membrane receptors optimal for rapid temporal processing useful for speech, and retain other areas better for processing with a larger time window (also useful for speech). If these areas were 'modularized' genetically this means only that genetic variation could proceed independently in these areas, but it does not mean that the areas, in maturity, might not directly commingle their physiological and functional processing, for a representation of speech that integrates the entire spectrum of time windows – the 'language faculty' is not identical with the area with the receptor tweak.

A third property observed in evolving systems is 'weak linkage' between modules allowing for recombination. The 'G-protein' signaling system is an example of this, where different extracellular signals may become attached to this common system linking the environment to fundamental cellular processes, allowing for recombination and integration of external signals to activate intracellular mechanisms. This is an interesting way of considering brain circuitry, both in the specific case of what is connected to what across species, and at the metaphorical level of function. Space precludes development of this idea, in this essay, but note the similarity of this concept to the idea of 'cognitive penetrability' that has produced a massive literature in diverse fields of psychology.

Finally, evolved cellular systems show exploratory behavior, particularly in development expressing a wider variety of metabolic and signaling possibilities than mature cells do. This is obviously a feature of organisms in which nervous systems must play a central role, and is one of the central areas of study in cognitive science. Exploratory behavior is rarely considered systematically as an evolutionary phenomenon in cognitive science, however, with a few tantalizing exceptions: for example, modeling of the 'Baldwin effect' in language evolution. Burghardt's *The Genesis of Animal Play* (2005) is a beautiful example of a systematic cataloging of the causes and possible functions of a particular type of exploratory behavior both in phylogeny and ontogeny.

All of these properties in concert produce facilitated variation, 'evolvability', organisms robust and stable in the

face of environmental challenges. The systems which have been examined systematically so far are the general cellular physiology of organisms and the conservation and variation of the basic body plan. It seems to me, however, that this is a very attractive way to structure questions about brain and cognitive development.

Endless minds

Developmental science needs an evolution-based theory, but if the view of evolution is not current and sophisticated, there's no point to it. The choices offered by evolutionary psychologists and Chomskian linguists on the one hand and 'extreme' connectionists on the other do not employ any of the power of the evo-devo approach. In caricature, the first argue that the tiniest detail of adaptive behavior and its committed circuitry could be directly spelled out by the genome with little attention to the conserved structures that must underlie any cognitive capacity or the constructive effects of the environment. The second group imagines the brain as an initially uninstructed, uniform network, with no attention to its known mechanistic heterogeneity and the strong likelihood that evolution has written biases into the architecture of what may be analyzed, recombined and explored.

The evo-devo insight has suggested that the focus in evolutionary biology should be moved from the species, individual and gene, to the stable coordination of information transmission across generations. Information is transferred by robust and flexible mechanisms that can be identified at multiple levels of analysis, from cellular biology to behavior. Development can no longer be viewed as a simple passage from the embryo to the mature organism directed by the information encoded in the genes, but rather a structured collaboration between the information in the organism and the environment.

References

Atallah, H.E., Frank, M.J., & O'Reilly, R.C. (2004). Hippocampus, cortex, and basal ganglia: insights from computational models of complementary learning systems. *Neurobiology of Learning and Memory*, **82**, 253–267.

Barkow, J.H., Toobey, J., & Cosmides, L. (Eds.) (1995). *The adapted mind: Evolutionary psychology and the evolution of culture*. Oxford: Oxford University Press.

Burghardt, G. (2005). *The genesis of animal play*. Cambridge, MA: Bradford Books, MIT Press.

Buss, D.M., & Schmitt, D.P. (1993). Sexual strategies theory: an evolutionary perspective on human mating. *Psychological Review*, **100**, 204–232.

Darwin, Charles (1859). *The origin of species*. A Variorum Text. Ed. Morse Peckham. Philadelphia, PA: University of Pennsylvania Press.

Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.

Callaerts, P., Halder, G., & Gehring, W.J. (1997). Pax-6 in development and evolution. *Annual Review of Neuroscience*, **20**, 483–532.

Carrol, Sean B. (2005). *Endless forms most beautiful: The new science of evo devo*. New York: W.W. Norton and Co.

Elman, J.L. (1990). Finding structure in time. *Cognitive Science*, **14**, 179–211.

Fernald, R.D. (2004). Eyes: variety, development and evolution. *Brain, Behavior and Evolution*, **64**, 141–147.

Field, D.J. (1994). What is the goal of sensory coding? *Neural Computation*, **6**, 559–601.

Finlay, B.L. (2005). Rethinking developmental neurobiology. In M. Tomasello & S. Slobin (Eds.), *Beyond nature–nurture: Essays in honor of Elizabeth Bates* (pp. 195–219). Hillsdale, NJ: Lawrence Erlbaum Publishers.

Finlay B.L., Cheung, D., & Darlington, R.B. (2005). Developmental constraints on or developmental structure in brain evolution? In Y. Munakata & M. Johnson (Eds.), *Attention and performance XXI: Processes of change in brain and cognitive development* (pp. 131–162). Oxford: Oxford University Press.

Gerhart, J., & Kirschner, M. (1997). *Cells, embryos and evolution*. Malden, MA: Blackwell Science.

Goldstein, M.H., King, A.P., & West, M. (2003). Social interaction shapes babbling: testing parallels between birdsong and speech. *Proceedings of the National Academy of Sciences*, **100**, 8030–8035.

Gould, S.J. (2002). *The structure of evolutionary theory*. Cambridge, MA: Harvard University Press.

Greenough, W.T., & Bailey, C.H. (1988). The anatomy of a memory: convergence of results across a diversity of tests. *Trends in Neurosciences*, **11**, 142–147.

Jablonka, E., & Lamb, M. (2005). *Evolution in four dimensions*. Cambridge, MA: MIT Press.

Johnson, M.H., & Morton, J. (1991). *Biology and cognitive development: The case of face recognition*. Oxford: Blackwell.

Keller, M.C., & Miller, M. (2006). Resolving the paradox of common, harmful, heritable mental disorders. *Behavioral and Brain Sciences*, **29** (4).

Kirschner, M.W., & Gerhart, J.C. (2005). *The plausibility of life: Resolving Darwin's dilemma*. New Haven, CT: Yale University Press.

Land, M., & Nilsson, D.-E. (2001). *Animal eyes*. Oxford: Oxford University Press.

Pearson, H. (2006). What is a gene? *Nature*, **441**, 399–401.

Teramitsu, I., Kudo, L., London, S.E., Geschwind, D.H., & White, S.A. (2004). Parallel FoxP1 and FoxP2 expression in songbird and human brain predicts functional interaction. *Journal of Neuroscience*, **24**, 3152–3163.

West-Eberhard, M.J. (2003). *Developmental plasticity and evolution*. Oxford: Oxford University Press.

Wilkins, A.S. (2001). *The evolution of developmental pathways*. Sunderland, MA: Sinauer Associates.