ELSEVIER
Available online at www.sciencedirect.com
SCIENCE DIRECT®
Developmental Review xxx (2006) xxx–xxx
DEVELOPMENTAL REVIEW
www.elsevier.com/locate/dr

Evolutionary developmental psychology: Current status and future directions

David C. Geary *

Department of Psychological Sciences, 210 McAlester Hall, University of Missouri at Columbia, Columbia, MO 65211-2500, USA

Received 20 February 2006

Abstract

The field of developmental psychology is part of a continuum of disciplines, from cell biology to cultural anthropology, that are focused on understanding developing and potentially evolving phenotypes; the reciprocal interactions between genetics and experiences produce variation in developing phenotypes and this variation is the grist for evolutionary selection. The articles in this issue provide cutting edge and multidisciplinary analyses of developing and potentially evolving phenotypes in areas that are of central interest to developmental scientists, including mother–infant attachments, stress responses in children, social cognition, and life span development. The articles and other recent works signal the reemergence of developmental psychology as an evolutionarily informed, multidisciplinary field. In this view, it is not about nature versus nurture or biology versus psychology, it is about tackling difficult problems at multiple levels of analysis, each of which has something to contribute and none of which is sufficient in and of itself.

Keywords: Evolution; Development; Evolutionary psychology; Experience; Epigenetic

> the secret to understanding evolution is to first understand phenotypes, including their development and their responsiveness to the environment. West-Eberhard (2003, p. 28).

* Fax: +1 573 882 7710.
E-mail address: GearyD@Missouri.edu.

0273-2297/$ - see front matter © 2006 Published by Elsevier Inc.
doi:10.1016/j.dr.2006.02.005

Developmental psychology is the study of behavioral (i.e., object exploration), social (e.g., rough-and-tumble play), cognitive (e.g., language), and physical (e.g., pubertal growth) traits or phenotypes and the mechanisms that influence phenotypic change during the life span. The mechanisms that guide developmental change involve the reciprocal relations between gene expression and the individuals' internal (e.g., hormones) and external (e.g., parent–child conflict) environments. There is nothing in this description of developmental psychology that is unusual and there is nothing that is inconsistent with an evolutionary approach to development (Alexander, 1990; West-Eberhard, 2003). Indeed, West-Eberhard places the developing phenotype at the core of evolutionary change: "Adaptive evolution is a two-step process, first the production of phenotypic variation (by development), then selection. If the phenotypic variation has a genetic component, then selection produces evolutionary change" (p. 29). Thus, if we define our field in terms of the developing *and* potentially evolving phenotype, developmental psychology readily flows into a continuum of disciplines that are seeking to answer the many of the same questions, albeit at different levels of analysis (e.g., cell biology, embryology, and neurobiology) (West-Eberhard, 1998). At all levels, the study of development includes identification of species-typical patterns of phenotypic change, the sources of genetic and environmentally mediated variation within the species-typical range, and easily accommodates research on related species (see also Scarr, 1992, 1993).

Sex differences illustrate the basic point. Across species, including humans, sex hormones influence whether the embryo develops as a male or a female (Tanner, 1990); patterns of gene expression and thus later functional competencies in the developing and mature brain (Arnold et al., 2004; Good et al., 2003); and, post-natal biases in social behavior (Cohen-Bendahan, van de Beek, & Berenbaum, 2005). At the same time, the individuals' internal (e.g., exposure to viruses) and external (e.g., social competitors, food availability) environment can substantively influence the expression of sex and other hormones and through this gene expression and thus the developing phenotype and later social behaviors (e.g., Goldizen, 2003; Stearns & Koella, 1986). By adulthood, these multifactorial influences result in heritable and environmentally induced variation in parental behavior and forms of behavioral competition for mates, among other traits, which in turn results in variation in reproductive outcomes and the evolvability of associated phenotypes (Darwin, 1871; Pomiankowski & Møller, 1995). A full understanding of sex differences and all other naturally occurring variation requires identification of important phenotypes and the multiple genetic, hormonal, ecological, and social factors and their interactions that effect phenotypic expression and development.

Current contributions

Each of the articles in this issue provides a fine example of a theory-driven multi-level analysis and through this defines the current status and implications for future directions of the emerging field of evolutionary developmental psychology. More accurately, these contributions illustrate how the research programs of developmental psychologists can contribute to and gain from theoretical perspectives and research programs traditionally associated with other disciplines.

Maestripieri and Roney open the series with a primer on the value of comparative research for making inferences about a species' evolutionary history and for differentiating between evolved and functionally adaptive phenotypes and phenotypes that are expressed for other reasons. They nicely illustrate the utility and importance of this approach by describing evidence for continuity between aspects of human development and that of other species of primate. They show, for instance, that functional (e.g., maintaining proximity to mother for safety reasons) and behavioral (e.g., distress at separation from mother) components of the mother–infant attachment system in humans are also evident in Old World monkeys (from Africa and Asia) and great apes (e.g., chimpanzees, *Pan troglodytes*). These species are phyologenetically related to humans (i.e., share a common ancestor) and therefore these components of attachment almost certainly have a deep evolutionary history. Other components of the human attachment system, especially use of mental models of attachment figures, are not well elaborated or may be entirely absent in nonhuman primates and thus these components of attachment may be a recent evolutionary adaptation in humans. In addition to providing a solid means of making inferences about evolved adaptations, comparative research allows for the study of development (e.g., mother–offspring attachment) in a natural context and under experimentally varied conditions, neither of which are common or always possible with much of the research conducted on human development in Western settings.

Flinn provides a unique illustration of an evolutionarily informed human research program conducted in a natural context, with his 18 year anthropological field study of children's stress responses and family functioning. The setting is a village in the West Indian island of Dominica, and has allowed Flinn and his colleagues to study children's stress and related responses in multiple contexts and across time. These assessments provide an invaluable addition to laboratory based studies of the same phenomena and have yielded many important findings. Children's stress and immunological systems are especially sensitive to social context and in particular to unanticipated and difficult to resolve family conflict. The lowest basal stress hormone levels are found for children living in families with their biological mother and at least one other biological relative (e.g., father, grandmother), whereas children living with a single mother, in a blended family, or with distant relatives show the highest basal stress hormone levels. The empirical assessments provide tests of alternative hypotheses concerning whether stress responses in social contexts are an evolved adaptation or simply a by-product of an overtaxed system that has evolved to cope with other types of stressors (e.g., predators). Of course, chronic and uncontrollable stressors from any source have potentially devastating consequences for physical and psychological health. But, can more moderate levels of social stress have a beneficial effect?; specifically, are aspects of the stress response an evolved adaptation that results in changes in memory and social problem solving that facilitate the generation of strategies for coping with these stressors? Flinn believes this to be the case, and so do I.

Ellis, Jackson, and Boyce complement Flinn's contribution, and begin with an overview of the basic biological structures and functions of the human stress-response systems. These are the systems that are common to all humans and in fact individuals in many other species – indicating a very deep evolutionary history—and function to allow individuals to physically (e.g., changes in blood flow), cognitively (e.g., increased fear and alertness), and behaviorally (e.g., fight or flight) respond to threats to their well being. Ellis and colleagues, however, focus on individual variation in stress response within the constraints of these species-typical systems. This normal variation is produced by a combination of genetic and environmental factors, including heritable individual differences in sensitivity to the same stressor (see also Belsky, 2005). As Ellis and colleagues describe, variation of this sort can be random genetic or environmental "noise" in terms of past selection pressures; something akin to error variance in an Analysis of Variance, where selective pressures (e.g., predatory risks) are main effects and individual differences are error variance. An important and almost certainly correct proposal—consistent with Flinn's model—is that at least some of this normal variation can be understood as being maintained by selection pressures that favor social and ecological niche seeking (see also Scarr & McCartney, 1983).

For humans and all highly social species, the dynamics of social living result in a multi-niche social ecology and this in turn creates a context in which variation in phenotypes (including those related to stress response) and biases in behavioral niche seeking can evolve. Ellis and colleagues use West-Eberhard's (2003) model of phenotypic development to explore the different forms of gene-environment interactions that can result in behavioral variation within the species-typical range and related individual differences in niche seeking. Variation in the stress-response system is then integrated with life history theory (see below) in ways that allow us to better understand human individual differences in sensitivity to early developmental stressors and opportunities, and to later differences in timing of reproductive maturation (e.g., age of menarche) and behavior (see also Belsky, Steinberg, & Draper, 1991; Vigil & Geary, 2006). The combination of their model and Flinn's proposals generates many testable empirical predictions regarding the relations among early social experiences, developing sensitivities of the stress-response systems to social conditions, and long-term reproductive development and behavior. The combination also allows us to better understand normal variation in these phenotypes, as well as the conditions that result in phenotypes outside of the species-typical range and are thus pathological.

Bjorklund begins with a brief overview of the history of evolutionary and developmental biology and their theoretical separation in the early 20th century and recent reunion and reintegration, as exemplified by West-Eberhard (2003). As noted, understanding the relations between plasticity in developing phenotypes and the evolution of these phenotypes provides a broad and very rich theoretical framework for the study of human development. Bjorklund nicely illustrates the importance and utility of this perspective, with discussion of epigenetic maternal effects, such as, environmental influences on maternal phenotypes that influence her developing offspring and often her grandoffspring. As an example of how maternal *experiences* can be transmitted to offspring, it is common for offspring of nutrient-deprived plants to allocate more growth-related resources to root production, and offspring of light-deprived plants to allocate more resources to leaf production (Sultan, 2000; see also Alekseev & Lampert, 2001; for an analogous mechanism in the crustacean *Daphnia*). In other words, offspring in these species develop in ways that are well adapted to maternal *experiences*. Bjorklund provides many more examples, and focuses on the more interesting potential for maternal behavior to affect the developing and potentially evolving behavioral and cognitive phenotypes of her offspring, elaborating on the earlier proposals of Baldwin (1896) and Waddington (1942).

Bjorklund's most intriguing proposal is that we can use human enculturation of chimpanzees and other apes as a means to test hypotheses about epigenetic influences during human behavioral, social, and cognitive evolution. These are nongenetic maternal influences on developing offspring that contribute to individual differences in behavioral and cognitive phenotypes during development. By influencing the developing phenotype of offspring, these nongenetic maternal effects contribute to the variation on which selective pressures act. To illustrate how these effects might have operated during human evolution, Bjorklund reviews the important differences in the social behavior and perhaps the social cognition of chimpanzees raised by humans and those raised in natural conditions. Chimpanzees raised by humans show several competencies, such as referential pointing (i.e., use of this gesture to direct the attention of another individual to a distant object), that are not common in chimpanzees raised in the wild. The difference means that at least some chimpanzees have the potential to develop this competency, but this potential is never realized in natural settings. If there are heritable individual differences in the potential of chimpanzee juveniles to learn referential pointing, given appropriate maternal input, and referential pointing provides a social and reproductive advantage later in life, then we have the conditions that could eventually result in the evolution of referential pointing without maternal input. In other words, this is a potentially important mechanism that relates behavioral and cognitive plasticity during development to the evolution of social behavior and cognition in humans.

The special issue closes with Figueredo and colleagues' sweeping model of human life history development and the sources of individual differences in this development (Figueredo, Vásquez, Brumbach, Schneider, Sefcek, Tal, Hill, Wenner, & Jacobs). Life history is a core area of evolutionary biology and is focused on the study of the suite of phenotypic traits that defines the species' maturational and reproductive pattern, such as length of gestation and typical age of first reproduction (Charnov, 1993; Roff, 1992). A suite of traits must be considered because of the trade offs involved in the expression of one phenotype versus another (Williams, 1957). The trade offs are commonly conceptualized in terms of a competitive allocation of resources (e.g., calories) to somatic effort, such as growth during development, or reproductive effort, that is, a focus on mating or parenting. Across and within species and in response to identifiable ecological and social selection pressures, life history traits tend to cluster together. For instance, high predation risks are associated with fast maturation, production of many offspring, and limited parental investment in each offspring (e.g., mice). The clustering of these traits and our understanding of the ecological and social pressures that contributed to their evolution and the experiences that influence their phenotypic expression within the species-typical range provide a theoretical framework that has the potential to unify many areas of developmental psychology.

Figueredo and colleagues use life history theory to organize human individual differences across an impressive range of social (e.g., criminal violations), personality (e.g., conscientiousness), neural (e.g., prefrontal cortex) developmental (e.g., age of menarche), and parenting (e.g., investment in children) phenotypes, among others. At one end is a constellation of behaviors that include low investment from their parents (e.g., father absence, low monitoring of behavior during adolescence) and in their children, early sexual activity, unstable social and sexual relationships in adulthood, and high risk taking for short-term gain. At the other end is a constellation of behaviors that include high investment from parents and in their children, delayed sexual activity, stable social relationships, monogamy, and a focus on long-term goals (e.g., college attendance). They integrate these individual differences with our understanding of variation in brain development and propose and present evidence consistent with the hypothesis that these differences can indeed be and placed on a single life history continuum. There is evidence that variation along this continuum is related to both heritable and experiential factors, some of which may include the stress-response mechanisms described by Ellis et al. and Flinn. In any case, from a life history perspective, variation along this continuum is consistent with the above noted niche seeking and is in no way an indicator of preferred or "bad to good" behaviors.

Conclusion

Evolutionary developmental psychology need not be a subfield of psychology or of development but rather can represent a frame of reference whereby evolutionary theory and multidisciplinary findings are used to more fully define and understand developing and potentially evolving behavioral (e.g., play), social (e.g., attachment), cognitive (e.g., theory of mind), and physical (e.g., menarche, brain maturation) phenotypes (West-Eberhard, 1998). The goal is to understand the reciprocal interactions between genes and experiences as these relate to species-typical phenotypic development and to normal variation within this range (Scarr, 1992). Each of the articles in this special issue, as well as other recent contributions (e.g., Bjorklund & Pellegrini, 2002; Burgess & MacDonald, 2004; Ellis, 2004; Ellis & Bjorklund, 2005; Geary, 2002), provides this form of evolutionary and multidisciplinary analysis, an approach that one day will be the norm (granted this may be 100 years from now) for developmental psychologists and other developmental scientists.

References

Alekseev, V., & Lampert, W. (2001). Maternal control of resting-egg production in *Daphnia*. *Nature, 414*, 899–901.

Alexander, R. D. (1990). Epigenetic rules and Darwinian algorithms: The adaptive study of learning and development. *Ethology and Sociobiology, 11*, 1–63.

Arnold, A. P., Xu, J., Grisham, W., Chen, X., Kin, Y.-H., & Itoh, Y. (2004). Sex chromosomes and brain sexual differentiation. *Endocrinology, 145*, 1057–1062.

Baldwin, J. M. (1896). A new factor in evolution. *American Naturalist, 30*, 441–451 536–553.

Belsky, J. (2005). Differential susceptibility to rearing influence: An evolutionary hypothesis and some evidence. In B. J. Ellis & D. F. Bjorklund (Eds.), *Origins of the social mind: Evolutionary psychology and child development* (pp. 139–163). New York: Guilford Publications.

Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialization. *Child Development, 62*, 647–670.

Bjorklund, D. F., & Pellegrini, A. D. (2002). *The origins of human nature: Evolutionary developmental psychology*. Washington, DC: American Psychological Association.

Burgess, R., & MacDonald, K. (Eds.). (2004). *Evolutionary perspectives on human development*. Thousand Oaks, CA: Sage Publications.

Charnov, E. L. (1993). *Life history invariants: Some explorations of symmetry in evolutionary ecology*. New York: Oxford University Press.

Cohen-Bendahan, C. C. C., van de Beek, C., & Berenbaum, S. A. (2005). Prenatal sex hormone effects on child and adult sex-typed behavior: Methods and findings. *Neuroscience and Biobehavioral Reviews, 29*, 353–384.

Darwin, C. (1871). *The descent of man, and selection in relation to sex*. London: John Murray.

Ellis, B. J. (2004). Timing of pubertal maturation in girls: An integrated life history approach. *Psychological Bulletin, 130*, 920–958.

Ellis, B. J., & Bjorklund, D. F. (Eds.). (2005). *Origins of the social mind: Evolutionary psychology and child development*. New York: Guilford Publications.

Geary, D. C. (2002). Sexual selection and human life history. In R. Kail (Ed.), *Advances in child development and behavior* (Vol. 30, pp. 41–101). San Diego, CA: Academic Press.

Goldizen, A. W. (2003). Social monogamy and its variations in callitrichids: Do these relate to the costs of infant care. In U. H. Reichard & C. Boesch (Eds.), *Monogamy: Mating strategies in birds, humans and other mammals* (pp. 232–247). Cambridge, UK: Cambridge University Press.

Good, C. D., Lawrence, K., Thomas, N. S., Price, C. J., Ashburner, J., Friston, K. J., et al. (2003). Dosage-sensitive X-linked locus influences the development of amygdala and orbitofrontal cortex, and fear recognition in humans. *Brian, 126*, 2431–2446.

Pomiankowski, A., & Møller, A. P. (1995). A resolution of the lek paradox. *Proceedings of the Royal Society of London B, 260*, 21–29.

Roff, D. A. (1992). *The evolution of life histories: Theory and analysis*. New York: Chapman & Hall.

Scarr, S. (1992). Developmental theories of the1990s: Developmental and individual differences. *Child Development, 63*, 1–19.

Scarr, S. (1993). Biological and cultural diversity: The legacy of Darwin for development. *Child Development, 64*, 1333–1353.

Scarr, S., & McCartney, K. (1983). How people make their own environments: A theory of genotype → environment effects. *Child Development, 54*, 424–435.

Stearns, S. C., & Koella, J. C. (1986). The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. *Evolution, 40*, 893–913.

Sultan, S. E. (2000). Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science, 5*, 537–542.

Tanner, J. M. (1990). *Foetus into man: Physical growth from conception to maturity*. Cambridge, MA: Harvard University Press.

Vigil, J. M., & Geary, D. C. (2006). Family and community background and variation in women's life history development. *Journal of Family Psychology*, 20.

Waddington, C. H. (1942). Canalization of development and the inheritance of acquired characters. *Nature, 150*, 563–565.

West-Eberhard, M. J. (1998). Evolution in light of developmental and cell biology, and vice versa. *Proceedings of the National Academy of Sciences USA, 95*, 8417–8419.

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

Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. *Evolution, 11*, 398–411.