Developing Human Nature: “Development to” Versus “Development from?”

ABSTRACT: Evolutionary psychology (EP) emphasizes that socio-cultural experiences are constrained by the characteristics of the individual. Therefore, cultural experience acts on a nervous system biased to respond to in particular ways (i.e., human nature). For EP, evolutionary lineage and adaptive significance explain the development of such human nature (a “development to” approach). Gottlieb, and others in Developmental psychobiology (DPB), have explained the development of “instinctive” behavior patterns of a wide variety of animals using a “development from” approach. The DPB approach does not contradict a human nature that reflects an evolutionary heritage with adaptive value. We present three examples that demonstrate how a DPB approach to development accounts both for the expression of patterns specific to the individual as well as patterns that are species-typical (human nature, for humans) without shifting explanatory constructs and frameworks. © 2007 Wiley Periodicals, Inc. Dev Psychobiol 49: 788–799, 2007.

Keywords: culture; innate; experience; ethology; sociobiology; evolutionary psychology; evolution; genetics; parental care

INTRODUCTION

In 1963, soon to be Nobel Lauriat (1972) Niko Tinbergen tried to unite factions within the relatively young discipline of Ethology by proposing that the study of species-typical animal behavior could be focused on any combination of four quasi-independent questions. Questions could be asked about the evolution of the animal’s behavior patterns (phylogeny), the functions of the animal’s behavior (adaptation and use), the causes of the animal’s behavior (physiological mechanisms), and the development of the animal’s behavior (ontogeny). Tinbergen proposed that “causal” (physiological) research should examine the interaction between physiological mechanisms and social and physical environmental stimuli for the expression of species-typical behavior, a kind of ecological physiology. Ontogenetic research could include investigations of: both the precursors and prerequisites for the emergence of the behavior; transformations of the behavior with age; identification of phases during development when the developmental trajectories leading to the behavior were most sensitive to common events that could disrupt or confirm the trajectory; factors which constrain the plasticity of the behavior once it had become established. Each of these developmental processes likely involved the effects of experience. Tinbergen’s intent was to give equal value to these four questions in addressing the reasons why animals exhibit both species-typical and individually distinct behaviors. At that time, several British and American researchers (e.g., Hinde, 1959, 1960; Lehrman, 1953, 1956) were highly critical of Ethology’s typical argument that the development of species-typical behavior is innate and controlled by maturation and that the causal organization species-typical behavior is controlled primarily by endogenous mechanisms simply released or directed by stimuli. Thus, in Tinbergen’s formulation, experiential factors could play an important organizational and constructive role in both the development and causation of species-typical behavior.

In order to understand Tinbergen’s proposal, it is important to remember that Ethology emerged as a
discipline during the period when the “Modern Synthesis” (which united Mendelian genetics with Darwinian evolution) was forged in evolutionary biology. For Darwin, species were arbitrary boundaries imposed by humans on a seamless continuum of trait variation. Trait variability is the substrate upon which natural selection and other evolutionary mechanisms operate to create the populations with different traits that we categorize as species. However, the particular variants of traits had to be somewhat heritable and stable across generations if natural selection was to accumulate complex adaptive matches of the species’ traits to its environment. Evolution by natural selection requires a reliable cross-generation transmission of traits. Mendelian genetics helped account for the inheritance of traits and the “Modern Synthesis” linked trait variability to the characteristics of genes.

The relationship between the genotype (“traits encoded in the genome”) and the phenotype (“the traits that are actually observed”) was considered unidirectional. The phenotype (individual’s physiology, anatomy, behavior, and developmental characteristics) can exhibit adaptations in response to environmental changes and challenges but these often are reversed when the environmental challenge subsides. Evolutionarily significant adaptations are heritable changes in physiology, anatomy, behavior, and development that are transmitted across generations and last even when the environmental challenge disappears. Genes code for those traits that were heritable and sensitive to natural selection and variability of genes yields variability of traits. Since genes control phenotypes and are the components of the germ cells that help form the offspring, genes reliably transmit trait information across generations. In the modern synthesis, natural selection operates on phenotypes but indirectly influences gene frequencies. Hence, evolution could be defined as changes in gene frequencies.

Within this frame, ethologists argued that because species-typical (instinctive) behaviors exhibit a phylogenetic history and serve important adaptive functions they must be the result of natural selection. If they result from natural selection, then the development and causal expression of species-typical behaviors must be controlled by gene mechanisms controlling the developmental organization of the nervous system. Development would have to be controlled to ensure achievement of the adaptively important species-typical behaviors (a “development to” approach). Thus, for some ethologists, evolutionary history and adaptive function of species-typical behaviors determined both the type of experiments designed to examine, and the kind of answers expected to be obtained from, developmental and causal questions.

Tinbergen’s (1963) intent was unsuccessful. Konrad Lorenz (1965) (sharer of the 1972 Prize) reasserted that natural selection must be the frame within which all species-typical (instinctive) behavior should be examined and understood. For Lorenz and his followers, phylogeny and adaptation had to dictate the form of the investigation and explanation of the causation and development of an animal’s behavior. Instinctive behaviors were organized by genetic control of the formation of neuromotor programs (fixed action patterns and appetitive behaviors) that were triggered or released by external stimuli (sign stimuli) that matched genetically controlled perceptual programs (innate releasing mechanisms). The development of these programs reflected a genetically controlled program involving an intercalation of learned with innate information to insure the adaptive outcome. The mechanism for such dictation was the presumed character of the genomic influence on the development of the individual. Those genes common across individuals resulted in the development of species-typical behaviors and those genes unique to individuals resulted in the development of inter-individual variability in “instinctive” behavior. Environmental influences either severely disrupted normal development (e.g., disease, malnutrition, abuse, neglect) or operated through genetically determined periods during development (“critical periods”) when the trajectory of genetically controlled development could be fostered or hampered (the intercalation of learned and innate information). Again, natural selection was the source of these periods and for the genes that controlled them.

For most ethologists, the primary question was how did adaptation control the causes and development of the animal’s behavior? Phylogenetic comparisons of closely related species revealed the ancestral forms (similarities across comparisons) as well as those forms that were uniquely selected to fit the species’ environment. Systematic observations of the context of behaviors gave clues to their adaptive significance at the level of the species. A special mechanism of development at the level of the individual ensured the expression of these evolutionarily significant behaviors. Learning might account for certain of an individual’s behaviors but this mechanism was different from that controlling the development of instinctive behaviors.

EXTENSION TO HUMAN DEVELOPMENT

By the 1970s, Bowlby (1969), Eibl-Eibesfeldt (1975), and others successfully expanded the Lorenzian approach to the study of human behavior. Such “Human Ethology” characterized the development and causation of what was considered human species-typical behavior or human nature (e.g., attachment, aggression, fears) by identifying innate traits (as defined by: very early appearance during
development, not trained or practiced before expression, universal across cultures, etc.) that were likely constrained by natural selection forces that had operated during evolution. These traits did not derive from cultural experience or individual learning.

Bowlby also introduced the phrase “environment of evolutionary adaptedness” (EEA) to refer to the environment to which a particular evolved mechanism is adapted. An EEA is both the set of historically recurring selection pressures that formed a given adaptation and those aspects of the environment that were necessary for the proper development and functioning of the adaptation. Again, evolution is controlling development. For example, in the environment in which ducks evolved, attachment of ducklings to their mother had great survival value. Since the first moving thing that a duckling was likely to encounter was its mother, a mechanism that evolved to form an attachment to the first moving thing would properly function to form an attachment to the mother. In non-EEA environments, the mechanism can malfunction and form an attachment to a human or watering can instead. Note that this approach assumes adaptation (attachment of ducklings to their mother had great survival value) based on the observation of imprinting and then uses the observation of imprinting to prove the adaptiveness of the phenomenon. Such tautology can be broken by a “development from” approach described below.

Edward O. Wilson (1975) proposed that modern biology was dividing into two distinct approaches to explanation. Behavior could be understood either as caused by mechanisms derived from the expression of genes during development or as the consequence of natural selective forces that shaped the genes controlling the behavior. So, although genes controlled the individual, natural selection controlled the genes. Wilson was certain that these two approaches to behavior (that he dubbed the new science of “sociobiology”) would render redundant human sociology, economics, politics, and psychology. Wilson’s notions relied heavily on Hamilton’s (1964), Maynard Smith’s (1964, 1977), and Williams’ (1966) genetic (essentially economic) models of the presumed reproductive costs and benefits to the individual genotype of different complex behavioral functions such as social communities and altruism.

Wilson (1978) solidified his argument that human behavior (not specific behaviors but broad personality traits like, aggression, sexual orientation, certain moral and social values, belief in god(s), need for religious institutions and creeds) could be accounted for by molecular biological analyses of the genetic determination of the development and causation of behavior and sociobiological analyses of genetic costs and benefits (in terms of reproduction) that led to the evolution of the behavior. By the 1990s, human Sociobiology had morphed into “Evolutionary Psychology (EP)” (e.g., Buss, 1999) primarily because Sociobiology had been tainted with an apparent racist slant. Individual and species-typical characteristics in mate selection, social skills (leadership, altruism, etc.), cognitive abilities (talents, intelligence, etc.), personality (risk-taking, shyness, etc.), and such were accounted for by presumed selective pressures thought to operate during the Pleistocene evolution of humans. Each trait was presumed to reflect a specific neural module (network) dedicated to its expression. Since culture and technology changed more rapidly than evolution, ancient human traits could be in conflict with modern societal customs and requirements. For example, it is likely that the density of populations created by agricultural and architectural technology lead to increased contact with “strangers” resulting in increased frequency of individual stress reactions.

EP and Human Ethology did reemphasize a common problem in the study of human culture: socio-cultural experiences are constrained by the characteristics of the individual, possibly those that are unique to the individual as well as those that “connect” the individual to the species. Therefore, any explanation as to how a socio-cultural experience can have the effect it does must admit that experience acts on something of the individual that must be biased to respond to such experience in particular ways. Since EP turns to evolutionary lineage and adaptive significance for an explanation of such bias, it promotes the notion of a human nature created by evolution (especially natural selection) as distinct from a “cultural nature” (unique to a particular culture) created by learning. Thus, cultures might differ in the type of language spoken but language was a universal characteristic of human nature (as was male aggression, female coyness, xenophobia, belief in god(s), following leader, etc.).

To be sure, at no time did any researcher of EP, Human Ethology, or human Sociobiology deny the influences of culture, social training, or experience on the expression of individual behavior or personality traits. Rather, these influences were thought to be distinctly different from genetically determined developmental mechanisms fostered by natural selection. The particulars of a culture were considered to be acquired by training, imitation, teaching, and frequently involved practice. Hence, it was likely that at times human nature and culture could be in conflict. Moreover, individual differences in talents, intelligence, social skill, sexual preference, and such were the consequence of individual differences in the genetics controlling their development and these, too, could be in conflict with culture (e.g., homosexuality). The genes were thought to specify the predisposition for the traits whereas the environment was believed to affect the extent
of their manifestation. Hence, any manifestation of a trait was a consequence of gene--environment interaction.

EP proposed that culture itself, and the social training and experience provided to individuals, frequently was constrained or promoted by the power of natural selection operating through the selected genes. Human nature consists of “certain inherent response tendencies” inherent in the organization of the nervous system and “[t]he environment can have no systematic effects” unless there are “programs” or “modules” in the individual’s nervous system which permit the environmentally influence (see Gaulin & McBurney, 2004, pp. 5 & 355). So, even the acquisition of cultural particulars required naturally selected sensitivities to experience, a notion very reminiscent of Lorenz’s innate-learned intercalation. Research was necessary to identify these different sources of influence on the individual’s development so that social and cultural processes could be aligned with “human nature” for the betterment of the individual and society. Consider this notion in relation to some common conceptions of gene--environment interaction in human psychology (cf., Moffett, Caspi, & Rutter, 2006).

For example, individuals who were maltreated as children were more likely to be diagnosed as adults with antisocial personality or conduct disorder if they had a polymorphism for low expression of the monoamine oxidase A (MAOA) genotype compared to those with a genotype resulting in high levels of expression of MAOA (Caspi et al., 2002). In this common gene--environment interaction approach, we have no explanations for why some individuals with both the “predisposing” polymorphism and the “predisposing” child abuse did not become adults with antisocial personalities (we are to presume that they are functioning with the disorder). Also, left unexplained is how some individuals without either predisposing condition, nevertheless did develop an antisocial personality as adults. What appears to be a developmental study does not reveal the influences that directly affect the creation of individually unique differences in developmental trajectories.

From this perspective, human (and all animal) traits were the consequence of biologically determined propensities (think natural selection of genes and genetic control of the development of anatomical mechanisms—modules—of behavioral traits) interacting with socially and culturally constructed environmental events (think working mothers, literacy, geographic separation of extended families, enculturation, etc.). Knowledge of these two sources of influence could be ascertained by examination of the adaptive function and evolutionary history of the species of interest. This would sharpen the developmental focus to seeking the earliest manifestations of the trait of interest and what factors assure that the trait develops appropriately (a “development to” the trait of interest). The specific character of such gene--environment interaction could result in the development of normal or abnormal traits.

Experience during development plays either a permissive role (permitting normal development of species-typical traits or human nature) or a disruptive role (interfering with normal development and resulting in abnormal traits) in this “development to” approach. Knowing the genetically controlled propensities for particular traits would mean that the experiences of an individual would be controlled to prevent expression or permit expression of those traits appropriately matching a culture’s needs. In this perspective, experience does not play a constructive role in the development of the species-typical trait or human nature. Rather, the final product is presumed to be preset as “encoded,” as a “module,” as an “instinct,” or as a wired program (see Bateson and Mameli, this volume).

From the alternative perspective that Tinbergen tried to incorporate into Ethology, all animal traits “developed from” an extensive transaction of the developing individual with environmental influences throughout the lifespan. The focus of developmental research was on how the transactions with the social and physical environment of a trait of the individual at one phase resulted in the maintenance of that trait, its loss, or its transformation into a different trait in the subsequent phase of development and so on through the lifespan. Gilbert Gottlieb was one of the few researchers studying animal behavior for whom this alternative emphasis and approach was paramount and for whom Tinbergen’s (1963) proposal was apropos.

**EVIDENCE FOR THE “DEVELOPMENT FROM” APPROACH**

Gottlieb’s research on the development of the species-typical social preferences of certain species of duck gave much empirical power to this approach (Gottlieb, 1971). In addition, the “development from” approach revealed nonintuitive and counter-intuitive (i.e., from knowledge of the adaptation and phylogenetic history of the trait) experiential influences on the development of species-typical behavioral traits (Michel, 2007). Using this approach, it is possible to discover experiential factors that are not intuitively obvious, bear little resemblance to customary notions of learning (e.g., Hein & Diamond, 1983), and may be functionally discontinuous with the behavioral system under study (e.g., Bekoff, 1992). Gottlieb’s theoretical writings (Gottlieb, 1992, 2002) argued against the prevailing notion that natural selection created developmental programs and for the notion that developmental processes (and not simply genetics) created the variability among traits upon which natural
selection could operate. Essentially, the argument was one of emphasis and approach to research (Lehrman, 1970).

However, Gottlieb’s notion was consistent with the recognition that what is selected during evolution is not a specific state of the individual’s system but mechanisms that can produce a range of states in response to a range of conditions. The adaptability of the individual creates a range of alternative phenotypes (the norm of reaction, Schlichting & Pigliucci, 1998) on which selection can operate. Since the phenotypic norm of reaction for any individual genotype could be known only after it had developed in all combinations of conditions and durations of exposure to those conditions, development harbors a potentially extensive range of variability. Gottlieb recognized that basing evolution on developmental variability eliminates the teleology inherent in the “development to” evolutionary explanations and permits random mutations to eventually stabilize the development of existing phenotypes.

Interestingly, modern molecular biology toppled the notion that genes are simple causal agents of variability; rather, they are part of a network of developmental causes that lead to the manifestation of traits. Information in the genome is intertwined with ecological influences from the environment in different ways at different periods throughout the lifespan (cf., Gerhart & Kirschner, 1997; Gilbert, 2006; Kirschner & Gerhart, 2006; Raff, 1996; Schlichting & Pigliucci, 1998). Genes have become part of a complex system (network) of causes that operates throughout the lifespan to produce phenotypic variability. Cells are chemical manufacturing plants controlled by an intricate and dynamic set of chemical messengers that travel within and between cells to turn specific genes on or off, and the timing of these actions is important. Such “gene switching” sets the steps in motion that lead to protein synthesis or other key changes in cell function.

The layer of biochemical reactions that turns genes on and off is called the “epigenome” and the transduction of environmental stimuli into neurobiological processes permits the environment to become a part of the epigenome that turns genes on or off. Such environmental transduction defines an “experience” for an individual. There are many ways by which environmental information can affect the epigenomic process and new ways continue to be discovered. The epigenome plays a major part in heredity, as well as development and health, because molecular biological research has demonstrated that cells can transmit information to daughter cells through non-DNA (epigenetic) inheritance. These epigenomic processes begin before conception during the formation of germ cells (eggs and sperm) and continue throughout the lifespan. They do not alter the DNA (there is no environmental directing of mutations) but rather they influence how genetic information is used during development.

Because the epigenome can change according to an individual’s environment and is passed reliably from generation to generation, there has been a revolutionary change in biological thinking about heredity and evolution. Evolution is not changes in gene frequencies. Genes are part of a network of developmental causes that lead to the manifestation of traits that have general properties in common across individuals while retaining individual differences. Evolution is change in the frequencies of alternative developmental causes that yield variations in developmental trajectories (a phrase that is more cumbersome than “changes in gene frequencies” but nevertheless more correct). Consequently, modern evolutionary biology has turned to developmental biology as a source for information about how trait variability (the substrate upon which natural selection and other evolutionary mechanisms operate) can emerge during development. This approach is called “evo-devo” (e.g., Fox Keller, 2002; Gilbert, 2006; Jablonka & Lamb, 2005; Raff, 1996; West-Eberhardt, 2003). Oddly, some evolutionary psychologists have assimilated evo-devo to mean the old concept that evolution controls development. On the contrary, evolution by natural selection cannot occur without the variability created by development. Natural selection operates at the phenotypic level and the openness of developmental processes to experiential influences creates the individually unique trajectories that result in phenotypic variability.

During the past 50 years, developmental psychologists like Gottlieb have demonstrated that the neural circuits involved in species-typical and individually specific behavior patterns of a wide variety of mammals, birds, reptiles, fish, insects, mollusks, etc., are sculpted by experience involving effects on neuron receptor sensitivity and neurotransmitter productivity. In 1976, Gottlieb, 1976 described three developmental consequences of individual experience (Fig. 1): (1) induction, in which experience is necessary to alter expression of a trait; (2) facilitation, in which experience regulates (promotes or inhibits) the rate of developmental progression for the expression of a trait; (3) maintenance, in which experience sustains a trait in the repertoire of the individual. Experience is notoriously difficult to categorize and Gottlieb’s categories have problems. Although inductive experiences appear to have clear developmental consequences, facilitating experiences can appear to be mere fine-tuning of genetically programmed progression and maintaining experiences can appear to be irrelevant to development because the trait has already developed. However, both facilitating and maintaining experiential influences can have major consequences for development, equal in impact as those categorized as inductive.
Since the individual is an organized system, delaying or accelerating the rate of development among different features or traits (heterochrony) can ramify to affect the development and expression of other features. Heterochrony across the development of traits is considered a fundamental source for the production of new patterns of organization upon which natural selection can operate (de Beer, 1930; Gould, 1977). Distinctly different individuals can emerge from alterations in the relative rate of development among specific features or traits. Indeed, maintaining a trait beyond its developmental time frame or failing to maintain it for the typical extent of its time frame can have ramifications on the development and functional organization of other traits because the individual is an integrated system. Therefore, whether an experience can be categorized as maintaining, facilitating, or inducing the development of a trait often may depend on the type of measure that is used. The distinctions among Gottlieb’s categories of experiential influences on development are fuzzy at best.

The “development from” approach of Gottlieb and other developmental psychobiologists has revealed the surprising richness by which individual experience contributes to the development of species-typical behaviors in animals. We propose that the investigation of the development of human nature would benefit from adopting a similar approach because this approach uncovers the contributions of ubiquitous and nonintuitive experiences to development. It is these developmental mechanisms that create the variability in development that marks the character of human nature and upon which natural selection operated. However, since natural selection is differential reproductive success, only those traits that demonstrably affect reproduction and are reliably transmitted across generations can come under natural selection pressure.

If we are to determine whether experience influences the development of human nature and species-typical traits in other animals, then it must be demonstrated that these experiential influences: (1) contribute reliably to individual variability, particularly those that mark interindividual differences; (2) be reliably transmitted across generations; (3) contribute to the reproductive processes of the individual. Therefore, unless it can be demonstrated that variation on some trait (e.g., mathematical skill, belief in a supernatural being) directly or indirectly affects the development of species-typical behaviors.
reproductive success either positively or negatively, it will be invisible to natural selection (including sexual selection). Too often, a trait has been presumed to be species typical because it appears to be adaptive without any direct examination of how it affects reproductive success (cf., Annett, 1995; Michel, 1995). It is important to recognize that there are traits that are neither adaptive nor nonadaptive.

In order to help identify how experiential influences on developmental trajectories can create the variability upon which natural selection can operate, we present the following three examples.

**Effects of Experiential Differences in Maternal Care on Offspring Development**

Individual differences in maternal behavior have been demonstrated in many mammals and birds including humans, other primates, and rodents. Many studies have demonstrated that early differences in parental behaviors can have an impact on the offspring’s adult behavioral functioning via the influences of these maternal care differences on the offspring’s neural, molecular, and hormonal mechanisms. In rodents, licking the offspring (particularly anogenital licking) is essential to survival. A rat dam’s licking of the anogenital region of her pups (AGL) is important for the development of the ability of the pup’s nervous system to control processes of urination and elimination (Gubernick & Alberts, 1983). Also, the AGL-stimulated urination and defecation is ingested by the dam and that permits her to recycle more than 70% of the fluids and nutrients that she loses through nursing. Individual differences in maternal pup-licking and other behaviors affect the development of the offspring’s sexual behavior (Moore, 1984; 1992), visual system’s functions (Landi et al., 2007), emotional coping ability such as risk-taking and stress reactions (Fish et al., 2004).

Low frequency maternal pup licking (typical of the way that dams treat their female offspring, Moore & Morelli, 1979) is associated with early pubertal onset in female offspring whereas high frequency maternal pup licking (typical of the way dams treat their male offspring) is associated with a masculinization of the female offspring’s external genitalia. Male and female pups that receive high frequency maternal licking become adults who exhibit lower levels of anxiety in stress-inducing situations as compared to pups of dams who engaged in low levels of pup licking. The specific pattern of pup licking affects the development of the molecular processes involved in the hypothalamic-pituitary-adrenal activation via its influence on DNA methylation (a process that “turns off” genomic activity) in hippocampal nerve cells. By affecting the methylation of the pup’s DNA, the licking pattern alters the production of receptors for glucocorticoids which are important for the hippocampal regulation of the hypothalamic control of both the autonomic nervous system and the pituitary’s control of the adrenal secretion of glucocorticoids (Meaney & Szyf, 2005). The activation of the autonomic nervous system and the secretion of glucocorticoids affect the rat’s responsiveness to social and emotion-inducing situations. Thus, individual differences in maternal care affect the development individual differences in the offspring’s sensory, social, emotional, and sexual functioning. Are these maternal-induced differences in development transmitted across generations?

These individual differences in maternal behavior have been shown to be transmitted from mothers to their female offspring (Fleming et al., 2002). In rodents, there is an intergenerational transmission of maternal licking of the offspring. Female offspring born to mothers who engage in high frequencies of pup licking become high frequency lickers of their offspring when they become mothers; whereas, female offspring born to mothers who engage in low frequency pup licking become low frequency lickers when they become mothers. Cross fostering (Champagne, Curley, & Meaney, 2007) and more direct manipulation of maternal licking (Fleming et al., 2002) studies show that this generational transmission is mediated by the care they received during the nursing period. Moreover, as adults, those females exposed to low frequencies of licking have a reduced sensitivity to estrogen in the medial preoptic area (MPOA) because they exhibit lower levels of estrogen receptor alpha expression. This receptor expression emerges during infancy and is sustained into adulthood (Champagne et al., 2006).

Within the promoter region of the estrogen receptor alpha gene, there are several sites at which methyl groups can bind to cytosines within the DNA (methylation). Comparison of offspring of low and high licking moms showed that the ER alpha promoter region of those with low licking females have higher levels of methylation. This methylation prevents the binding of certain factors (e.g., Stat-5a) that normally activate transcription of ER alpha. Thus, low frequencies of maternal care are associated with high levels of DNA methylation and low levels of ER alpha expression in the MPOA in the offspring which leads to their low frequency of maternal licking when they become mothers. Thus, experience during development induces epigenetic changes in the offspring’s neuroendocrine functioning which result, in females, in stable cross-generational individual differences in maternal care. The development of individual differences in rat maternal behavior and emotional reactivity seems to be a good example of the inductive aspect of experience and the maternal experiences do induce cross-generational differences in development.
However, it is unknown whether these experience-induced differences in behavioral phenotypes are “visible” to natural selection. If not, they are developmental exaptations available for potential selection. Since heterochrony in development can be important for evolution, maintaining a feature or trait means that it can participate with others in the developmental emergence of some new features or traits. Thus, if experience maintains a trait beyond the developmental phase in which it may be most appropriate, the trait could become an important exaptation for the emergence of a new species. For example, juvenile males in many species of rodent exhibit allopupal care of pups. Such parental behavior disappears after puberty (adult males of many species kill pups and hence most rodents are uniparental). There are several experiential conditions (specific circadian light and/or temperature conditions) that seem to maintain the male’s allopupal care into adulthood. These experiential conditions (which are associated with particular habitats) may have been the foundation for the evolution of biparental care in certain species (Michel & Tyler, 2007). Maintaining experiences can be a necessary condition for the development of many other features. Maintenance of a feature or trait may prevent reorganization of the system as a result of further experience. For example, Moore, Dou, and Juraska (1992) observed that the frequency of AGL that a rat pup received preweaning positively affected the frequency of juvenile ano-genital self licking. Thus, the individual maintains the AGL experienced during the juvenile period at a level related to that provided by the mother during the nursing period. This high-level self-AGL seems to promote the development of puberty in the male. Thus, this experience-influenced development of individual differences is associated with reproductive processes that can be affected by natural selection.

Experience in Infant Sensorimotor Skill Development

Although other species exhibit lateral biases in their limb use and some exhibit a population shift of the bias to predominant right- or left-limb use (Halpern, Gunturkun, Hopkins, & Rogers, 2005), humans exhibit a species-typical pattern of a striking population bias toward right handedness. Several genetic models have been proposed to account for this right bias (Annett, 1995; McManus & Bryden, 1992). Most human infants begin to exhibit reliable hand-use preferences (with a population level right bias) when apprehending objects by 6–7 months of age as a consequence of several prenatal and neonatal posturally induced sensorimotor experiences (cf., Michel, 2002). The infant’s prehension handedness transforms into a handedness for unimanual manipulation of objects by 9–11 months. By 12–14 months of age, the infant’s handedness has blossomed into a complex role-differentiated bimanual handedness. Thus, via a set of ubiquitous self-generated experiences infants develop either a right- or left-handedness by the end of their first year (Michel, 2007). Despite this common developmental trajectory toward handedness, by 14 months a substantial minority of infants has not yet exhibited reliable handedness. Thus, there are two major patterns of infant handedness development: those with and those without a handedness status by 14 months.

Also, during the period from 6 to 14 months, infants are acquiring several other sensorimotor skills that have been proposed (e.g., Bruner, 1973; Piaget, 1952) as forming the basis of more symbolic intellectual abilities (concept formation, cause and effect reasoning, knowledge of object properties, etc.). Object “storage” is a sensorimotor ability developing during this age period, that Bruner proposed, was the first sign of representational thinking in the infant. Before the acquisition of object storage skills, infants typically drop the one or two manually acquired objects when they are challenged with the presentation of additional attractive objects. By dropping objects, infants lose not only the objects but also the capability of comparing object property similarities and differences and the ability to engage in the kinds of constructive actions that three or more objects afford. By “storing” the objects already acquired in retrieval places (to the side, lap, mouth, etc.) when challenged with additional objects, the stored objects can be readily retrieved and compared with and combined with the newly acquired objects. However, “storing” requires that the infant have the ability to “represent” the object’s position, although it is no longer in the sensory field, so that it can be retrieved.

We have found that the development of object storage skills occurs sooner for infants with a reliable hand-use preference (right or left) during this age period than for those infants without a reliable handedness (Fig. 2). All infants eventually acquire object storage skills, so the infant’s handedness status merely facilitates the development of object storage. Nevertheless, those infants with handedness have acquired a representational skill (storage) a month or two sooner than those without handedness. Although it is unclear whether such differences among the development of different traits during infancy has any impact on the infants traits later in development, it is likely that infants with handedness are employing representational processes within a different developmental background of other sensorimotor skills than those without handedness. That means that it is likely that these differences in developmental trajectories ramify to affect a broad range of individual differences in adults.
The relative ubiquity of the experiences contributing to the development of infant handedness ensures the “heritability” of the developmental change in the initiation of representational and its relation to other abilities. What is unknown is whether such differences in the developmental trajectories of individuals with and without handedness during the 6- to 14-month period affects subsequent adult reproductive success and hence would be “visible” to natural selection.

Experience Influenced Reproductive Cycles in Ring Doves

The ring dove breeding cycle can be considered as three tightly coupled cycles (Michel, 1986): the physiological progression of reproduction from the formation of gametes, the fertilization of the eggs, the laying of the eggs, and the establishment of incubation, feeding the young and weaning the young at fledging; the hormonal cycle of the parents (successful reproduction requires participation of both parents); and the behavioral cycle of the parents. Since the same hormones that regulate the physiological progression of reproduction also augment the expression of specific behaviors, hormones can coordinate the parents’ behavior so that their behaviors are in synchrony with one another and with the appropriate phases of each of their physiological cycles.

Parents must synchronize their behavioral expression not only with the physiological events essential for reproduction, but also with one another so that the behavior of each parent either complements or supplements that of the other. Antagonistic behavior or phase differences in behavioral expression disrupt the progression of the cycle and reduce breeding efficiency. Because hormones that are secreted by parents help to regulate the temporal organization of both the physiological and behavioral aspects of a breeding cycle, behavioral synchrony between mates can be assured by having the secretion of some hormones sensitive to the stimuli provided by the behavior of the mate. Indeed, stimuli provided by the mate can affect the hormonal status of their partner indirectly, through feedback from the behavior performed by the partner in response to the mate-produced stimuli (self-stimulative experience).

A ring dove undertaking its first reproductive cycle must establish coordination of its behavioral changes with the hormonally governed progress of its reproductive physiology and it must establish hormonal and behavioral synchrony with its mate. It has long been known that there are differences in breeding efficiency between reproductively naive and experienced doves and these differences are significant enough to be visible to natural selection. Yet, reproductively naive ring doves usually successfully complete their first reproductive cycle even though they may never have performed any of those behaviors previously (e.g., sitting on eggs, feeding young). The successful completion of a first cycle occurs primarily because the dove’s experiences during early phases of its first cycle provide the necessary background for appropriate orientation to, and behavior with, nest, eggs, and young all of which appear later in the same cycle. That is, each of the phases of the dove’s initial cycle may create the

FIGURE 2 Trajectories for the development of storage ability of 6–14 month old infants with and without a hand use preference.
experiences needed for the dove to complete subsequent phases of the cycle.

This can be demonstrated by experimentally creating hormonal states typical of certain of the phases of the cycle. Reproductively experienced doves readily establish incubation within 2 hr when they are injected with progesterone and placed in a cage with a similarly experienced and injected mate and a nest with eggs. In contrast, reproductively naive doves do not establish incubation until 5–7 days later under identical conditions (Michel, 1977). Similarly, reproductively naive doves do not brood and feed young when injected with prolactin whereas reproductively experienced doves do (Lehrman, 1971). By manipulating a dove’s experience with phases of a cycle previous to those associated with the hormonal state specific for incubation or feeding phase, we can discover what phases a dove must experience in order to behave as an experienced dove in that hormonal state. Using this technique, it was shown that the establishment of incubation after egg laying during the dove’s first cycle depends on the experience provided by the earlier phase of nest construction (Michel, 1986). The self-stimulative experience of nest construction prepares the dove’s nervous system to be more sensitive to the hormone (progesterone) secreted during the incubation phase of the cycle.

The dove does not “learn” to incubate eggs by participating in nest construction. Rather, the experience provided by feedback from the self-generated stimuli associated with nest construction is essential for preparing the nervous system to be sensitive to the stimuli provided by the eggs. Those stimuli become important for the initiation of incubation behavior. Moreover, feedback from the experiences created by the self-generated stimuli associated with the incubation of eggs prepares the dove’s nervous system to brood the young after the eggs hatch (Moore, 1976). Incubating the eggs provides the tactile stimulation important for the secretion of prolactin which not only prepares the dove’s crop for feeding the young but also maintains the incubation behavior before hatching. Reproductively experienced males who had been separated from their mate by a glass plate 3 days after they had established incubation will continue to secrete prolactin, despite their lack of contact with eggs. Observing their mate incubate seems sufficient to stimulate prolactin secretion. Reproductively naive males require 8 days of incubation (about two-thirds of the incubation phase of the reproductive cycle) before observation of the incubating mate is sufficient to stimulate prolactin secretion. Thus, stimuli from other modalities (e.g., visual, auditory) associated with the tactile stimuli that stimulate prolactin secretion during the course of a first breeding cycle, also can come to stimulate prolactin secretion in subsequent cycles (Michel & Moore, 1986).

Therefore, during subsequent cycles, these associated stimuli provide some assurance that the male’s physiological condition will be appropriate for the brooding and feeding of the young despite any disruptions in his incubation behavior. Thus, during the first breeding cycle, the reproductively naive dove’s nervous system is exposed to changing levels, ratios, and temporal patterns of hormonal secretions. Also, the dove’s nervous system is exposed to temporal patterns of social and physical environmental stimulation. Much of the stimulation that the dove experiences is generated by its own behaviors either directly through feedback mechanisms associated with the monitoring of its own performance (self-stimulative experience) or indirectly by affecting the pattern of stimulation provided by the mate (self-generated experience).

Of course, the reproductive cycle of the ring dove is even more complicated than this brief account can indicate (see Michel, 1986). However, these few examples demonstrate the importance of individual and ubiquitous experience in the organization of a ring dove’s reproductive cycle that is visible to natural selection. Unfortunately, too little work is being conducted on unraveling the pathways from the transduction of the stimuli into experiential events that play a role in the functional organization of the individual’s nervous system and its influence on, and responsiveness to, patterns of hormonal secretion. Perhaps, that is because there appears to be too little similarity between ring dove reproduction and the phenomena that are typically of interest to humans.

CONCLUSIONS

In all three examples cited above, the developmental transformations and expressions of behavior are constructed by a dynamic, but empirically specifiable, relation of the individual’s experience (with the social and physical environmental) to the individual’s developing neurobiological and physiological systems. The developmental processes for both species-typical and individually unique behavioral traits are created by the same mechanism. This mechanism involves the dynamic relation between the social and physical environment, as these are transduced into physiological processes, and the developing neurobiological and physiological systems. The development of human nature and human culture derive from this same mechanism. Therefore, separating culture and nature is meaningless for explaining development.

The species-typical phenotypes of birds and mammals have developmental trajectories which permit many opportunities for experiential influences as revealed by developmental psychobiological research using a
“development from” approach. Moreover, developmental psychobiological research has demonstrated how frequently animals transmit information to their offspring by behavioral means (behavioral inheritance, Jablonka & Lamb, 2005). We inherit our genes from our parents, but also, we inherit the environment—including diet (Mennella, Ziegler, Briefel, & Novak, 2006; Walker et al., 2007), specific social and physical experiences, habitat (West, King, & Arberg, 1988), and these inherited environments can alter how specific genes behave throughout the lifespan. EP has reminded us of the importance of investigating human nature but currently only developmental psychobiological research is providing answers to how development and evolution are related. We propose that a “development from” approach is capable of accounting both for the expression of patterns specific to the individual’s culture as well as patterns common to human behavior without shifting explanatory constructs and frameworks.

REFERENCES


