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## Children, childhood, and development in evolutionary perspective



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### ABSTRACT

We examine children, childhood, and development from an evolutionary perspective. We begin by reviewing major assumptions of evolutionary–developmental psychology, including the integration of “soft” developmental systems theory with ideas from mainstream evolutionary psychology. We then discuss the concept of adaptive developmental plasticity and describe the core evolutionary concept of developmental programming and some of its applications to human development, as instantiated in life history theory and the theory of differential susceptibility to environmental influence. We then discuss the concept of adaptation from an evolutionary–developmental perspective, including ontogenetic and deferred adaptations, and examine the development of some adaptations of infancy and childhood from the domains of folk psychology and folk physics. We conclude that evolutionary theory can serve as a metatheory for developmental science.

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### Introduction

The scope of developmental psychology has traditionally, and quite logically, been limited to the lifetime of the individual, from conception to death. Such a focus, however, ignores an important

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contributor to human development: its phylogenetic history. From this perspective, we agree with Konner (2010) that nothing in childhood makes sense except in the light of evolution.

The focus of this article is children, childhood, and development from an evolutionary perspective. Evolutionary thinking is not new in developmental psychology. The theories of many of the founding fathers of the field, including Wilhem Preyer, James Mark Baldwin, G. Stanley Hall, Sigmund Freud, Jean Piaget, Lev Vygotsky, and Heinz Werner, were influenced by Darwin's (and sometimes Lamarck's) ideas (see Morss, 1990). Some of these ideas were based on subsequently discredited conceptions (e.g., Haeckel's recapitulation theory), and evolutionary thinking fell out of favor among prominent child developmental theorists in the middle of the 20th century (John Bowlby and Jerome Bruner being notable exceptions), largely for two reasons. One was the "gene's eye view" of mainstream evolutionary psychology, with its apparent adoption of a form of genetic determinism – anathema to most developmental psychologists; the other was the initial focus of evolutionary psychology on adults, the individuals who do the reproducing.

Perspectives in both biology and developmental psychology have changed over recent decades, prompted by, among other things, the advent in biology of evo-devo (e.g., West-Eberhard, 2003), the formulation of epigenetic theories of inheritance and evolution (e.g., Dias & Ressler, 2013; Jablonka & Lamb, 2005; Meaney, 2010), and the explicit application of developmental–contextual models in an evolutionary framework in which development can best be described as a dynamic system, with structures (and behaviors) emerging over time as a result of the continuous and reciprocal bidirectional interactions between the child and all levels of life, from genes and brains through parents, peers, and the larger culture (see, e.g., Bjorklund, Hernández Blasi, & Ellis, in press; Bjorklund & Pellegrini, 2002; Geary & Bjorklund, 2000).

We propose that an evolutionary perspective can serve as a *metatheory* for developmental psychology – an overarching perspective that examines the distal and functional causes of behavior – which must be integrated with other more proximal causal explanations. As a metatheory, an evolutionary perspective organizes known facts parsimoniously, provides guidance to important domains, leads to new predictions, and unifies psychology with the life sciences (see Ketelaar & Ellis, 2000). Natural selection may have shaped the genomes of our ancestors, but genes are always expressed in a context, and such contexts serve as the proximal causes of development. Although an evolutionary explanation may capture the likely course of development and help predict which environments are most likely to result in what type of developmental trajectory, such a "plan" is not preformed but is implemented in real time by the actions of both micro- and macroenvironments on inherited genes (and other cellular machinery passed on through the generations).

In this paper we first look at some of the major assumptions of evolutionary–developmental psychology, including a rejection of the idea that evolutionary accounts of development necessarily reflect a form of genetic determinism; rather, we argue that evolutionary accounts of development involve bidirectional Gene × Environment interactions emerging dynamically over time. The role of plasticity in evolutionary explication is emphasized, and infants' and children's abilities to adjust their developmental trajectories based on environmental conditions are examined with respect to life history theory and related evolutionary–developmental perspectives. We then examine the concept of adaptation from an evolutionary–developmental perspective, proposing that some adaptations serve to benefit the organism immediately but disappear when they are no longer needed (ontogenetic adaptations), whereas others serve to prepare infants and children for life as an adult (in addition to life as children – deferred adaptations). We then provide examples of developmental adaptations from the domains of folk psychology and folk physics and conclude by arguing that evolutionary theory can serve as a metatheory for developmental psychology.

### **All evolved characteristics develop via continuous and reciprocal bidirectional gene–environment interactions that emerge dynamically over time**

One reason why developmental psychologists did not embrace evolutionary approaches was the taint of genetic determinism. Mainstream evolutionary psychologists proposed, essentially, that genes underlie domain-specific information processing mechanisms, which generate behavior (e.g., Tooby & Cosmides, 1992). Although mainstream evolutionary psychologists reject the label "genetic

determinists,” for many developmentalists (e.g., [Lickliter & Honeycutt, 2003](#)) the view from evolutionary psychology left little room for development or the role of the environment other than triggering evolved psychological mechanisms. Rather, these evolved, inherited mechanisms are viewed as “innate,” a concept that many developmental psychologists reject. Although “innateness” can be purely descriptive (e.g., present at birth), it tends to have a host of often ill-defined connotations, similar to the concept of “instinct,” which is also avoided by many developmental psychologists. This is illustrated by [Bateson \(2002, p. 2212\)](#), who wrote:

Apart from its colloquial uses, the term instinct has at least nine scientific meanings: present at birth (or at a particular stage of development), not learned, developed before it can be used, unchanged once developed, shared by all members of the species (or at least of the same sex and age), organized into a distinct behavioral systems (such as foraging), served by a distinct neural module, adapted during evolution, and differences among individuals that are due to their possession of different genes. One does not necessarily imply another even though people often assume, without evidence, that it does.

All this, of courses, harkens back to the classic nature–nurture issue, which lies at the center of any discussion of the role of evolution in behavior. No serious scientist today advocates either extreme pole of this dichotomy. Contemporary science has made it clear that nature (biology, genes) and nurture (environment, experiences specific to one’s social group) interact over development to produce phenotypes. There is really no other alternative. However, there is still substantial disagreement about the nature of this interaction, with most developmental scientists advocating a variant of *developmental contextual approaches* (e.g., [Gottlieb, 2007](#); [Lerner, 2006](#)). From these perspectives, all parts of the organism, as well as the whole organism itself, interact dynamically, requiring that one always view the organism–context as a unit, or a *dynamic system*, and realizing that there are multiple interacting levels of context. This is perhaps best reflected by *developmental systems theory*.

#### *Developmental systems theory*

At the core of developmental systems theory is the concept of probabilistic epigenesis: “individual development is characterized by an increase in novelty and complexity of organization over time—the sequential emergence of new structural and functional properties and competencies—at all levels of analysis as a consequence of horizontal and vertical coactions among its parts, including organism–environment coactions” ([Gottlieb, Wahlsten, & Lickliter, 2006, p. 211](#)) (In biology, epigenetics also refers to the complex biochemical system that regulates gene expression, see [Jablonka and Lamb \(2005\)](#)). A developmental systems view of development describes ontogeny as a process of continuous, bidirectional interaction between components at all levels of the developmental system, including the genetic, cellular, phenotypic, behavioral, ecological, and cultural (see e.g., [Gottlieb, 2007](#); [West-Eberhard, 2003](#)).

From this perspective, there are no genes “for” a specific trait, and genes are not granted a privileged role in development but are viewed as one integral part of the developmental system that requires input from and interaction with other components of the system to function properly. Thus, the interaction between genes and environment over development jointly contribute to the emergence of phenotypic characteristics (see [Goldhaber, 2012](#); [Lewkowicz, 2011](#)). Genes, then, do not provide “instructions” that are carried out by cellular machinery, but only have “developmental meaning” when considered in relation to the larger developmental context ([Oyama, 2000](#)). Further, all genetic and environmental influences depend on the extant phenotype being organized to accept them ([West-Eberhard, 2003](#)), and the modified phenotype incorporates these influences as development proceeds.

#### *Developmental systems theory provides an alternative explanation of “instinct”*

Application of developmental systems theory can be illustrated by examining imprinting in precocial birds. The Nobel Prize winning ethologist Konrad [Lorenz \(1937\)](#) demonstrated that geese (and other precocial birds) typically follow the first quaking, moving thing they encounter several hours after hatching and become “imprinted” to that object, usually their mother, but sometimes

another object, including Lorenz himself. Lorenz noted that such behavior occurred without prior experience and clearly had survival value, a classic example of an “instinct.”

A developmental systems perspective, however, questions the “no-experience-necessary” assumption, noting that species-typical prenatal experience contributes significantly to the emergence of such complex behavior. This point was illustrated by [Gottlieb \(1976\)](#), who tested auditory imprinting in ducks. Gottlieb showed that, shortly after hatching, ducklings would approach the call of their own species, but only when they had heard conspecific vocal calls before hatching. Even hearing the peeps of clutch mates or their own vocalizations was sufficient to produce the species-typical “imprinting” response. When the ducklings were prevented from hearing any vocalizations, they responded randomly. Thus, a classic demonstration of a “no-experience-necessary” instinct actually requires experience and is an example of (probabilistic) epigenetic development. The highly adaptive tendency to approach the maternal call is not preformed but emerges from the structured interaction of biological and experiential factors.

Following Gottlieb's work, numerous studies demonstrated alterations of species-typical behavior in young animals as a result of species-atypical experiences (e.g., [Kenny & Turkewitz, 1986](#); [Lickliter, 1990](#)). For example, [Lickliter \(1990\)](#) showed that providing extra visual stimulation to bobwhite quail embryos, days before they would normally receive such stimulation, resulted in subsequent enhanced visual discrimination abilities but impaired auditory responding (they failed to discriminate and approach their own species call when it was paired with that of a chicken). Presumably, early sensory stimulation serves to organize the young organism toward certain, usually adaptive outcomes; but when sensory experience is withheld, received earlier than is normative, or experienced in excess of species-typical levels, species-atypical patterns of development result. Animals' neurology, physiology, and sensory systems are coordinated with species-typical experiences, both pre- and post-natally, to reliably produce species-typical behavior (including what were once called “instincts”).

In shaping the developmental system that underpins important behaviors, such as filial attachment in precocial birds, a minimal amount of information needs to be built into the organism (e.g., preparedness to detect and respond to early auditory inputs), obviating the need to postulate genes “for” imprinting. As [Bjorklund and Ellis \(2005, p. 13\)](#) stated, “This genetic information is extensively scaffolded by species-typical features of the environment, and the phenotypic outcome is a predictable, emergent property of the total developmental system.”

#### *Soft versus hard developmental systems theory*

A challenge in applying developmental systems theory stems from the fact that it is not a single, unified theory; in fact, it is possible to recognize at least two versions of developmental systems theory—a “soft” version and a “hard” version—with vastly different implications for developmental science ([Del Giudice & Ellis, in press](#); [Frankenhuis, Panchanathan, & Barrett, 2013](#); [Robert, Hall, & Olson, 2001](#)). Soft developmental systems theory is essentially a theory of development. In this view, a developmental system comprises all the “resources” (genes, cellular structures, sensory experiences, physical parameters of the environment, and so forth) that contribute to the ontogeny of the individual organism. However, the organism remains the main biological entity, and evolutionary processes act on populations of organisms. In other words, soft developmental systems theory reconceptualizes the causal structure of development—for example by placing genetic inheritance in a broader perspective and emphasizing bidirectional effects—but is otherwise consistent with inclusive fitness theory and the logic of individual adaptation ([Pradeu, 2010](#)). Indeed, many developmentally-oriented extensions of evolutionary biology already incorporate the main tenets of soft developmental systems theory (e.g., [West-Eberhard, 2003](#)).

In contrast, hard developmental systems theory is not so much a theory of development as a radical alternative to mainstream evolutionary theory. In hard developmental systems theory, a developmental system comprises all the resources that produce the developmental outcomes that are *stably replicated* in that lineage. As a consequence, it is impossible to meaningfully distinguish between organism and environment, and what evolves are not populations of organisms but populations of replicating “organism–environment” systems. Such a holistic reconceptualization of natural selection makes adaptationist analysis all but impossible ([Pradeu, 2010](#)). This is because hard developmental systems theory is inconsistent with inclusive fitness theory ([Hamilton, 1964](#)): Selection is no longer

assumed to act on individuals that can be more or less genetically related with one another, but on whole developmental systems (comprising every recurring influence on development, including social and bio-geographical factors) for which there is no meaningful definition of reproductive success or relatedness.

In summary, developmental systems theory comprises two related but partially distinct approaches. Soft developmental systems theory is a developmentally oriented extension of mainstream evolutionary theory and is fully consistent with the metatheoretical framework of evolutionary biology. In contrast, hard developmental systems theory advances a radically novel theory of evolution and constitutes an alternative metatheoretical framework with little overlap with that of mainstream evolutionary biology and thus is not embraced in the biological sciences. Embracing soft developmental systems theory does not commit one to also adopt the assumptions of hard developmental systems theory. Unfortunately, the distinction between the soft and hard version of developmental systems theory is often obscured in the literature, leaving many researchers confused as to the exact implications of the theory (see [Frankenhuis et al., 2013](#); [Pradeu, 2010](#)).

As reviewed by [Del Giudice and Ellis \(in press\)](#), in practice, developmental psychologists employ developmental systems theory to invoke or explain: (a) multiple levels of analysis; (b) environmental effects on neurobiological systems; (c) reciprocal effects between individuals and contexts; (d) person–environment interactions; and (e) probabilistic relations between developmental antecedents and outcomes. All of these points fall within the domain of soft developmental systems theory, all are convergent with the assumptions of evolutionary–developmental psychology, and it is this version of developmental systems theory that we endorse.

#### *Developmental systems theory and plasticity*

Because of the complex and continuous interactions between genes and environment over the course of ontogeny, developmental systems theorists posit a high degree of developmental plasticity. Plasticity, of course, is relative, varies across individuals (see discussion below of Differential Susceptibility), and varies with the system under consideration. For example, plasticity in developmental systems that primarily interact with stable features of the environment (e.g., oxygen, gravity) should be strongly constrained by natural selection. By contrast, plasticity in developmental systems that interact with more changing or variable aspects of the environment (e.g., social status, predatory threats) should be favored by selection (e.g., [Geary, 2005a](#)).

Even when plasticity is maintained, it may only be for limited developmental periods. For instance, in the example given earlier of auditory imprinting in precocial birds, the window of sensitivity is relatively small. The chick needs to be able to distinguish the call of its mother from other females in the first days of life (or before) for survival. The window of sensitivity is larger for human language, for example, lasting several years, presumably due to the greater complexity of learning a language and the number of years required to do so. Plasticity for both systems is subsequently lost or reduced once the critical behavior (maternal vocal identification, one's mother tongue) is acquired, preventing subsequent experience from interfering with the execution of important survival-related abilities. Further, the extent to which children are able to modify their behavior or cognition as a function of experience (i.e., their plasticity) is age dependent ([Fischer, van Doorn, Dieckmann, & Taborsky, 2014](#)). Although natural selection favors phenotypic plasticity when environments vary over time or space, young organisms can be expected to delay plasticity (i.e., to postpone entraining alternative developmental trajectories to match local conditions) until they have had adequate time to sample cues to the state of their environment ([Frankenhuis & Panchanathan, 2011a, 2011b](#)).

In some cases, cues to the state of the environment are provided during the prenatal period, when plasticity is often substantial and with a narrow window of sensitivity. This is obviously seen in the well-known effects of teratogens on physical development during the embryonic period ([Moore & Persaud, 2003](#)), but experiences during the prenatal period can also influence subsequent postnatal functioning in potentially beneficial ways, referred to as *predictive adaptive responses* ([Gluckman & Hanson, 2005](#)). For example, higher levels of maternal stress hormones may signal a more dangerous or unpredictable environment. Human fetuses that are exposed to elevated levels of stress hormones during gestation later show higher anxiety and fearfulness, temperamental difficulty, impulsivity, reduced executive functions, impaired attention, higher aggression and risk-taking, and increased

basal activity and responsivity of the HPA axis in childhood (e.g., Glover, 2011; Pluess & Belsky, 2011; see also Sandman, Davis, & Glynn, 2013 for fetuses' adaptive response to maternal depression). In an innovative study that attempted to tease apart genetic from prenatal experiential factors, researchers used a prenatal cross-fostering design, in which pregnant women were either genetically related or unrelated to their child as a result of in vitro fertilization (IVF) (Rice et al., 2010). Children's "antisocial" behavior when between 4 and 10 years of age was significantly related to stress experienced by their birth mothers, whether they were genetically related to them or not. In total, prenatal exposures to maternal stress hormones may be preparing children for more harsh and unpredictable environments (see further discussion below in the section on *life history theory/developmental programming*). There is an active debate in literature, however, regarding the extent to which fetal programming only functions to help children survive the mortality window of infancy or actually regulates longer-term adaptive variation in life history strategies (e.g., Kuzawa & Quinn, 2009).

### *Evolved probabilistic cognitive mechanisms*

Despite the high degree of plasticity in many systems, most members of a species follow very similar developmental trajectories despite the seeming potential for change. The reason for such similarity is that individuals inherit not only a species-typical genome but also a species-typical environment. Moreover, a species-typical genome biases animals to seek out and create a species-typical environment. In developmental systems theory, this species-typical environment is referred to as the "ontogenetic niche" (West & King, 1987), which is defined as the set of ecological and social factors that are reliably inherited by members of a given species. Genes are always expressed in the context of this ontogenetic niche, which not only includes such physical parameters as temperature and humidity, light levels and cycles, and energy sources and their distribution, but also—for most children over our evolutionary history—a protective womb during the prenatal period, a nursing and nurturing mother after birth, and a social network of people to care for a helpless infant and dependent child. As children grew older, they had peers and likely siblings to interact with. These species-typical conditions constrain phenotypic development and diversity; they limit the contexts in which genes will be expressed – and thus the form and function of development over the life course.

Humans are "prepared" by evolution to process some information more readily than others (language, for instance); they are constrained, both by their biology and their physical and social environments (and by the interaction of endogenous and exogenous factors) in how they make sense of their world, with such constraints making it easier to process certain types of information. *But prepared is not preformed* (Bjorklund, 2003). Rather, such constraints are the products of selectively structured Gene  $\times$  Environment  $\times$  Development interactions that emerge in each generation, are influenced by prenatal as well as postnatal environments, and reflect the inheritance of developmental systems, not just genes. Consistent with this idea, Bjorklund, Ellis, and Rosenberg (2007, p. 22) proposed the concept of *evolved probabilistic cognitive mechanisms*:

"information-processing mechanisms that have evolved to solve recurrent problems faced by ancestral populations; however, they are expressed in a probabilistic fashion in each individual in a generation, based on the continuous and bidirectional interaction over time at all levels of organization, from the genetic through the cultural. These mechanisms are universal, in that they will develop in a species-typical manner when an individual experiences a species-typical environment over the course of ontogeny."

Evolved probabilistic cognitive mechanisms, such as those involved in perceptual narrowing and prepared fears to be discussed below, are presumed to have a genetically *monomorphic structure*, in that the genes and their products that participate in these structures are possessed by all members of the species. At the same time, many adaptations have a genetically polymorphic structure, and these will be discussed in the section on *adaptive individual differences*.

### *Perceptual narrowing*

Several examples of infants being born "prepared" to give special processing priority to some types of information that is modified as a result of experience can be seen in the phenomenon of *perceptual*

*narrowing*. For example, shortly after birth, infants can seemingly perceive most, if not all, of the phonemes found in all human languages, suggesting substantial biological preparation for infants to learn language. With increasing exposure to their mother tongue, infants lose their ability to discriminate among “foreign” phonemes, as they become increasingly skilled in recognizing the phonemes and stress patterns of the language they hear around them (Kuhl et al., 2006).

A similar pattern is found for infants’ ability to process human faces. Shortly after birth, newborns are especially attentive to faces, and they process faces differently than they do other visual stimuli. For example, newborns (Di Giorgio, Leo, Pascalis, & Simion, 2012), 1-month olds (Wakako, Wada, Yamamoto, Mohri, & Taniike, 2014), and 6-month-old infants (Pascalis, de Haan, & Nelson, 2002) process upright faces of both humans and monkeys more efficiently than upside-down faces. Young infants appear to have inherited a relatively fixed (less plastic) system for drawing their attention to the features shared by both human and monkey faces. By 9-months, however, after having daily experience looking at human faces but presumably none looking at monkey faces, infants give special status only to upright human faces. They process monkey faces much as they do non-face stimuli, showing no greater facility for upright versus up-side-down images (Pascalis et al., 2002), suggesting that the processing of faces becomes more specialized with experience (Lewkowicz & Ghazanfar, 2009; Pascalis et al., 2002). This was definitively shown in a study in which 6-month-old infants were regularly exposed to the faces of Barbary monkeys (*Macaca sylvanus*) for three months (Pascalis et al., 2005). When tested at 9 months, these infants were able to discriminate among different monkey faces, an ability that is lost for infants without such exposure. According to Pascalis et al. (2002, p. 1321) “the ability to perceive faces narrows with development, due in large measure to the cortical specialization that occurs with experience viewing faces. In this view, the sensitivity of the face recognition system to differences in identity among the faces of one’s own species will increase with age and with experience in processing those faces.”

A similar pattern is found for infants’ abilities to discriminate among faces of men and women (Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002) and between people of their own race versus those of another race (e.g., Kelly et al., 2009). Thus, initial perceptual biases, associated with specialized brain regions, orient infants to attend to and selectively process faces, although they initially make no distinction among faces from different species, genders, or races. This capacity changes with experience. In the process, infants lose some plasticity – the ability to process all “face” information equally. Perceptual narrowing with respect to processing faces is a good example of a plastic system that is sensitive to evolutionarily-significant variation. Recognition of one’s mother’s face cannot be preformed, but sensitivity to basic facial features and an evolutionarily-expected experience of being cared for by mother results in the critical ability to recognize her.

### *Prepared fears*

The concept of being “prepared” to process some information more efficiently (or at least differently) from others can be seen in the domain of emotion, specifically fear. Just as rats seem prepared to associate nausea with previously consumed food (Garcia & Koelling, 1966), monkeys more readily react fearfully after watching another monkey respond with fright to a snake than to a rabbit or a flower (Cook & Mineka, 1989). Human research suggests that we may be similarly biased to attend to evolutionarily-relevant stimuli and to readily acquire fearful responses to them under certain situations. For example, adults (Öhman, Flykt, & Esteves, 2001), children (LoBue, 2010), and infants (LoBue & DeLoache, 2010) more easily identify snakes or spiders from an array of flowers or mushrooms than the reverse. In other research, 9-month-old infants paid special attention to evolutionarily fear-relevant sounds (e.g., hissing snake, crackling fire) than to modern fear-relevant (e.g., bomb exploding, tires screeching) or pleasant (e.g., Beethoven or rock-and-roll music, horse neighing) sounds (Erlich, Lipp, & Slaughter, 2013).

Yet, infants and young children seem not to have an “innate” fear of snakes, but rather a tendency to associate them with fearful responses (LoBue & Rakison, 2013). This point was demonstrated in studies in which 7- to 9-month-old infants and 14- to 16-month-old toddlers watched videos of snakes and other animals (giraffes, rhinoceroses) (DeLoache & LoBue, 2009). Although the children initially showed no fear of the snakes, when they were shown brief video clips of snakes and other animals associated with either a happy or fearful voice, they looked longer at the snakes when they

heard the fearful voice than when they heard the happy voice. There was no difference in looking time to the two voices when they saw videos of other animals. DeLoache and LoBue (2009) interpreted these findings as indicating that infants are prepared to acquire a fear of snakes. However, like monkeys, infants are not born with such a fear, but rather they apparently possess perceptual biases to be attentive to certain classes of stimuli and to associate them with fearful voices, consistent with the idea of evolved probabilistic cognitive mechanisms.

Although being prepared to acquire fear responses to certain classes of potentially harmful stimuli has clear survival benefits, it also has costs. Many snakes, for instance, that people encounter will not be poisonous, and avoiding them, and other objects with snake-like features, incurs some expense (e.g., loss of a potential food source, extra effort to avoid contact). Another cost is the development of phobias. Humans' biases to become fearful of certain classes of stimuli, although usually adaptive, can result in some people, because of individual differences in temperament and experience (Craske, 1999), developing unreasonable fear. For example, people in developed countries acquire phobias of evolutionarily fear-relevant stimuli such as, spiders, snakes, darkness, and heights more readily than modern "dangerous" objects such as knives, guns, automobiles, and electric outlets (Seligman, 1971). These cost-benefit tradeoffs have resulted in easily acquired fears if exposed to potentially dangerous animals or contexts – thus yielding adaptive benefits – but these fears will not develop without such exposure, avoiding the costs of over-generalizing the response.

### Adaptive individual differences

The preceding discussion focused on the importance of exposure to species-typical environments in regulating species-typical patterns of development. However, physical and social environments are often complex and afford more than one way to survive and reproduce. Accordingly, theory and research in evolutionary biology have come to acknowledge that, in most species, single "best" strategies for survival and reproduction are unlikely to evolve. Instead, the "best" strategy normally varies as a function of both (1) the physical, economic, and social parameters of an organism's environment (e.g., food availability, predation rates, quality of parental investment, social competition) and (2) an organism's condition or relative competitive abilities in the population (e.g., age, body size, health, history of wins and losses in agonistic encounters). Consequently, just as a strategy that promotes success in some environmental contexts may lead to failure in others, the cost-benefits trade-offs of different strategies vary depending on an organism's internal condition and competitive status (including genotypic influences).

A crucial question is, to what degree should phenotypic variation be more developmentally contingent and plastic versus more strongly regulated by genotypic variation? The answer is not simple; indeed, what is typically found in organisms is a mixture of the two. Theoretical models suggest that one should often expect a balance between genetic and environmental determination of phenotypic individual differences. Depending on the structure of environmental variation, the costs and benefits of plasticity, and the life history of an organism, a given selection regime (for example one of temporally fluctuating selection) may maintain different proportions of developmental plasticity and genotypic variation (Del Giudice & Ellis, *in press*).

On the one hand, because the viability of different survival and reproductive strategies are context- and condition-dependent, natural selection tends to maintain *adaptive developmental plasticity*: neurobiological systems that reliably guide the development of alternative phenotypes (anatomical, physiological, behavioral) to match an organism's internal condition and external environments (see West-Eberhard, 2003). Developmental plasticity involves "durable biological change in the structure or function of a tissue, organ, or biological system" (Kuzawa & Quinn, 2009, p. 132). Importantly, adaptive developmental plasticity is a non-random process; it is the outcome of structured Organism × Environment interactions that were shaped by natural selection to increase the capacity and tendency of individuals to implicitly track both their internal condition and external environments and adjust the development of their phenotypes accordingly.

On the other hand, despite these apparent benefits of developmental plasticity, there can be substantial costs. First, there is the cost of producing and maintaining the appropriate regulatory and assessment mechanisms to support alternative patterns of development. Second, environmental



cues may have limited validity, and thus developmental plasticity in response to current conditions may fail to correctly predict future environmental conditions. Consequently, while adaptive developmental plasticity is widespread (see detailed discussion of developmental programming to follow), it is not always the best or only option. As an alternative to adaptive developmental plasticity, or in conjunction with it, natural selection may also maintain genetic variation as a solution to the critical adaptive problem of matching phenotypes to heterogeneous environments. In this case, different genetically-regulated phenotypes (i.e., alternative phenotypes that are influenced by major genetic effects) are better suited to one niche than another, such as littoral (i.e., shoreline) versus open-water zones of an aquatic environment, or sneaking versus fighting in mating competition.

There are a variety of circumstances in which genetic contributions to alternative phenotypes are likely to be favored by natural selection (see Mitchell-Olds, Willis, & Goldstein, 2007). When individuals inhabit multi-niche environments and they are able to choose the niche that best fits their phenotype, it may partly or fully obviate the need for developmental plasticity. Instead, a diversity of genetically-regulated phenotypes, which are specialized to the different social or physical niches, can thrive in this context (see Wilson & Yoshimura, 1994). In addition, genetically regulated phenotypes can be maintained through *balancing selection*, whereby selection for alternative phenotypes systematically changes across time, space, and population states (meaning there is no long-term optimal phenotype or level of expression of a phenotype). A common type of balancing selection is *frequency-dependent selection*, which occurs when the fitness of different phenotypes changes as a function of their frequency in a population (Maynard Smith, 1998). The most viable form of frequency-dependent selection is negative, selecting against a given phenotype as it becomes more common. For example, aggressive individuals may be very successful when they are surrounded by tame individuals. However, as aggressive individuals multiply and begin to “invade” the population, their reproductive success may drop as they now compete mainly with other aggressive individuals, and less aggressive individuals may then be favored because they do not suffer the costs of aggression. Balancing selection can also result from *heterozygote advantage* (when individuals who are heterozygous at a certain locus have higher fitness than either of the homozygous types) or from changes in selection pressures over time and space (*fluctuating selection*). Fluctuating selection pressures, by definition, weaken natural selection for any single, optimal phenotype and therefore enable higher rates of genetically-regulated phenotypic variation—both systematic and unsystematic. Specifically, fluctuating selection pressures enable balancing selection, on the one hand, and make it more difficult for natural selection to eliminate neutral and deleterious forms of variation, on the other.

The reproductive strategies of the male swordtail fish (*Xiphiphorus nigrensis*) provide an example of the importance of adaptive genetic variation, adaptive developmental plasticity, and their interaction. In the swordtail, three alleles at the *P* locus on the Y chromosome correspond to three modes in size distribution of mature males (small, intermediate, and large; Ryan, Pease, & Morris, 1992). Although all three genotypes perform the range of species-typical mating strategies, they do so at different size-related frequencies. Specifically, small, intermediate, and large males generally sneak, sneak and court, and court females, respectively. Size is the primary mediating mechanism in this species through which allelic variations influence mating strategies.

In determining alternative mating strategies, the key developmental event in male swordtail fish is gonadarche (maturation of the gonads). Specifically, the three alleles at the *P* locus differentially influence timing of gonadarche (e.g., immunoreactive neurons containing gonadotropin-releasing hormone first appear at 5 weeks of age in genotypically small males versus 11 weeks of age in genotypically large males; Rhen & Crew, 2002). In addition to these genetic influences, timing of gonadarche is also sensitive to a number of environmental factors, such as temperature (Borowsky, 1987a) and agonistic interactions with other males (Borowsky, 1987b). These environmental influences can result in genotypically small males that are larger than genotypically intermediate males, and alternative mating strategies correlate more strongly with size than with genotype (Ryan & Causey, 1989). In addition, mating strategies of male swordtail fish are competition-dependent in relation to interaction with other males. For example, males of intermediate size will sneak and chase females rather than court when in the presence of larger males.

In sum, both genomic and environmental factors influence timing of gonadarche, which in turn coordinates patterns of gene expression involved in the developmental cascade that induces sexual

maturation and halts or dramatically reduces growth. Timing of gonadarche strongly influences size, and size is a major developmental factor in entrainment of alternative mating strategies. At the same time, mating strategies are conditionally adjusted in response to current physical and social dimensions of the environment. Thus, although there are strong genotypic influences on size and developmentally-linked mating strategies, the development of the alternative phenotypes in fact emerges through a complex series of gene–environment interactions.

Contemporary evolutionary perspectives on development recognize the complex interaction of genes and environment, both over the lifetime of an individual and of an individual's ancestors. While avoiding the taint of genetic determinism, these perspectives acknowledge the important role of genes in ontogeny and phylogeny, as well as the central concept of modern evolutionary biology, inclusive fitness theory (that adaptation through natural selection operates on populations of organisms that are more or less genetically related to one another). At the core of an evolutionary–developmental perspective is that plasticity is an evolved characteristic; children, infants, and fetuses are sensitive to environmental conditions, which entrain their development in (potentially) adaptive ways. Such plasticity is constrained, however, both by species-typical genes and environmental parameters, producing reasonably predictable patterns of development. At the same time, different life experience interact with genetic variation to program aspects of development, and this is captured by life history theory, to which we turn to now.

### **Life history theory/developmental programming**

Life history theory is a branch of evolutionary biology that addresses how organisms allocate time and energy to the various activities that comprise their life cycle (e.g., Hill & Kaplan, 1999; Stearns, 1992). All organisms live in a world of limited resources; for example, the energy that can be extracted from the environment in a given amount of time is intrinsically limited. Time itself is a limited good; the time spent by an organism looking for mates cannot be used to search for food or care for extant offspring. Since all these activities contribute to an organism's evolutionary fitness, devoting time and energy to one will typically involve both benefits and costs, resulting in trade-offs between different fitness components (Williams, 1966). For example, there is a trade-off between bodily growth and reproduction because both require substantial energetic investment, and thus producing offspring reduces somatic growth. Each trade-off constitutes a decision node in allocation of resources, and each decision node influences the next (opening up some options, closing others) in an unending chain over the life course (Ellis, Figueredo, Brumbach, & Schlomer, 2009). This chain of resource-allocation decisions – expressed in the development of a coherent, integrated suite of physiological and behavioral characteristics – constitutes the individual's *life history strategy*.

Life history strategies are adaptive solutions to fitness trade-offs within the constraints imposed by physical laws, phylogenetic history, and developmental mechanisms (Braendle, Heyland, & Flatt, 2011). At the most basic level, the resources of an organism must be distributed between somatic effort and reproductive effort. Somatic effort can be further subdivided into growth, survival and body maintenance, and developmental activity (Geary, 2002). Developmental activity includes play, learning, exercise, and other activities that contribute to building and accumulating *embodied capital* – strength, coordination, skills, knowledge, and other qualities that will improve later survival and reproductive prospects (Hill & Kaplan, 1999; Kaplan, Hill, Lancaster, & Hurtado, 2000). Reproductive effort can be subdivided into mating effort (finding and attracting mates, conceiving offspring), parenting effort (investing resources in already conceived offspring), and nepotistic effort (investing in other relatives).

The critical decisions involved in a life history strategy can be summarized by the fundamental trade-offs between current and future reproduction, between quality and quantity of offspring, and – in sexual species – between mating and parenting effort (see Ellis et al., 2009; Hill, 1993). By delaying reproduction, an organism can accumulate resources and/or embodied capital, thus increasing the quality and fitness of future offspring; however, the risk of dying before reproducing increases concomitantly. When reproduction occurs, the choice is between many offspring of lower quality and fewer offspring of higher quality. Although intensive parental investment is a powerful way to

increase the embodied capital (and long-term prospects) of one's descendants, the fitness gains accrued through parenting must be weighed against the corresponding reduction in mating opportunities and costs to parents and future offspring. Different life history strategies solve these problems in different ways by determining how organisms allocate effort among fitness-relevant characteristics. The same basic framework can be used to describe differences between species, as well as differences between individuals of the same species.

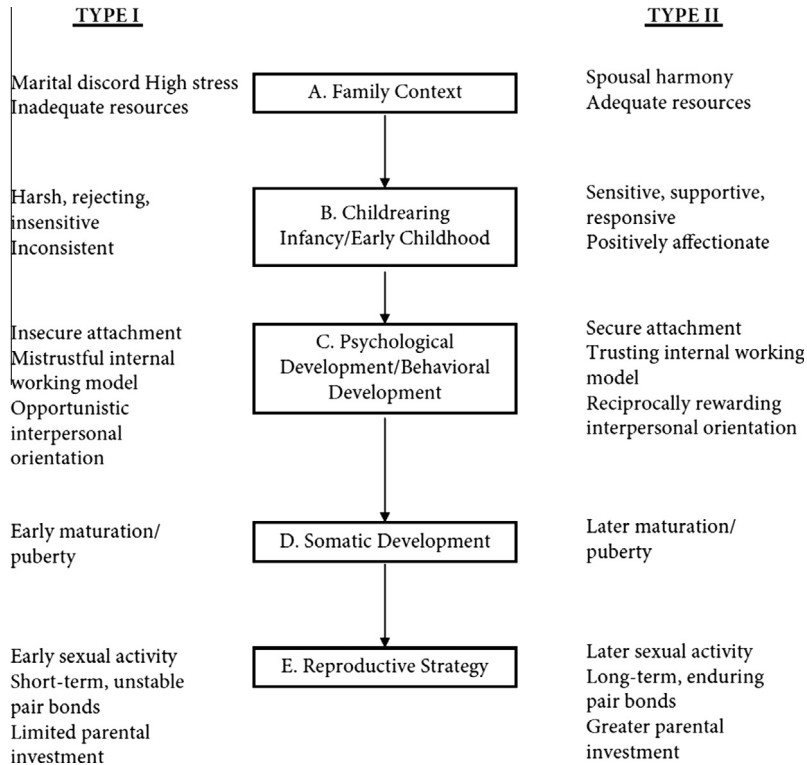
At the broadest level of analysis, life history strategies vary on a dimension of *slow* versus *fast*. Some people adopt slower strategies characterized by later sexual development and debut, a preference toward relatively stable pair bonds, an orientation toward longer-term investments and outcomes, and allocation of resources toward enhancing the growth and long-term survival of both oneself and one's offspring (i.e., embodied capital). In contrast, others display faster strategies characterized by the opposite pattern (see Belsky, Steinberg, & Draper, 1991; Ellis et al., 2009). Fast life history strategies are comparatively high risk, focusing on mating opportunities (including more risky and aggressive behavior), maturing and reproducing at younger ages, and producing a greater number of offspring with more variable outcomes.

Males and females encounter different reproductive opportunities and constraints that result in sex-specific patterns of mating effort and parental effort (Trivers, 1972) that underlie variation in life history strategies. Because of the higher maximal male rate of reproduction in most species (e.g., males can potentially sire many offspring in a short time span, as well as for a more extended period of their lives than females can), males usually undergo stronger sexual selection than females; that is, their reproductive success is more variable than that of females (for humans, see Hammer, Mendez, Cox, Woerner, & Wall, 2008). This pattern of differential variation is nearly universal (for a discussion of the few exceptions, see Brown, Laland, & Bergerhoff Mulder, 2009) and means that males, more than females, have been selected for high mating effort, including high-risk, high-stakes behaviors that leverage access to mates. Indeed, human males everywhere are more violent, homicidal, and risk-prone than are females, especially when such risks involve physical hazards (e.g., Archer, 2009; Byrnes, Miller, & Schafer, 1999; Cross, Copping, & Campbell, 2011), and are more motivated to obtain access to multiple sexual partners (reviewed in Okami & Shackelford, 2001). Because male reproductive success is ultimately constrained by the ability to access, attract, and retain females, men's life history strategies tend to be especially attuned to the demands and desires of females and their ability to successfully engage in intrasexual competition (James & Ellis, 2013; James, Ellis, Schlomer, & Garber, 2012).

The other side of the coin is that lower maximal reproductive rates bias females toward higher parental effort than males. Because of (1) higher minimum levels of parental effort by mothers than fathers (i.e., the long duration of gestation and considerable energetic investments of pregnancy and lactation, particularly during the early years of life when children are most vulnerable to mortality), and (2) the fact that maternal investments in gestation and lactation cannot readily be substituted by the parental or nepotistic efforts of other people, mothers are more critical than fathers to offspring survival. This sex differences has been well documented across human societies, where mothers have a much larger and more consistent impact on the survival of children than do fathers (Sear & Mace, 2008). As a result of their greater parental investment, females are ultimately constrained by the resources that they can extract from the environment, their relatives, and their mates in order to successfully produce and rear offspring; accordingly, female life history strategies tend to be especially attuned to the nature of the local ecology and levels of stress and support in and around their home environments (James & Ellis, 2013; James et al., 2012).

### *Psychosocial acceleration theory*

Based on life history theory, Belsky et al. (1991) advanced a landmark theory linking childhood experience, psychological developmental, somatic development, and reproductive strategies. Their *psychosocial acceleration theory* posited that (a) ecological conditions and family dynamics shape children's early attachment patterns and behavioral development and, through these developmental processes, subsequent pubertal development and reproductive strategy; and (b) this environmentally sensitive developmental system evolved as a means of matching individuals to their environment in a manner that promotes survival and reproduction across varying ecological contexts (see Fig. 1).



**Fig. 1.** Diagram of major components of Belsky et al.'s (1991) psychosocial acceleration theory. (From Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialization. *Child Development*, 62, 647–670.)

According to the theory, “a principal evolutionary function of early experience – the first 5–7 years of life – is to induce in the child an understanding of the availability and predictability of resources (broadly defined) in the environment, of the trustworthiness of others, and of the enduringness of close interpersonal relationships, all of which will affect how the developing person apportions reproductive effort” (p. 650). Psychosocial acceleration theory proposes that, over the course of our evolutionary history, individuals growing up under harsh or unpredictable family conditions may have benefitted from accelerated physical maturation and engaging in behaviors consistent with a faster life history strategy (i.e., earlier sex and reproduction, more risky sexual behavior, investment in quantity over quality of offspring). A shortened reproductive timetable in this context may have increased fitness by increasing the probability of producing at least some offspring that survive and reproduce. In contrast, individuals growing up in relatively benign and supportive family environments may have reliably increased their reproductive success by delaying reproductive maturation and engaging in behaviors consistent with a slower life history strategy. In such environments, deferring reproduction would allow individuals to acquire the embodied capital (i.e., strength, coordination, skills, knowledge) necessary for successful intrasexual competition for mates and subsequent provisioning of high-quality parental investment to offspring (Ellis, 2004). In total, the model posits that the local ecology, mediated by parental rearing strategies, should affect not only psychological and behavioral outcomes but also the allocation of bodily resources to somatic growth. Thus, a critical prediction of psychosocial acceleration theory is that early rearing experiences should influence the timing of pubertal maturation.

Three lines of evidence, derived from prospective longitudinal studies, support the critical pubertal timing prediction made by Belsky et al. (1991). First, greater familial warmth/positivity, parental

approval, and closeness/cohesion predict later pubertal maturation in girls (e.g., Ellis, McFadyen-Ketchum, Dodge, Pettit, & Bates, 1999; Graber, Brooks-Gunn, & Warren, 1995). Second, greater parent–child conflict and coercion predict earlier pubertal maturation in girls (e.g., Belsky et al., 2007; Costello et al., 2007). And finally, the more harmonious and less conflict-ridden the spousal relationship, the later pubertal maturation occurs in girls (e.g., Ellis & Graber, 2000; Saxbe & Repetti, 2009). In addition, there is a substantial literature demonstrating that childhood sexual abuse is associated with earlier pubertal development in girls (e.g., Trickett, Noll, & Putnam, 2011). Consistent with the earlier discussion of sex differences, these effects of family and ecological context on pubertal timing have been specific to females. At the same time, while these effects have emerged reliably in the developmental literature, they have typically been small in size (see discussion below of Differential Susceptibility), reflecting multiple influences on the development of life history strategies, including genetic influences.

Psychosocial acceleration theory has also been experimentally tested in rats using a cross-fostering design. Quality of maternal investment in rats tracks ecological conditions, with higher levels of stress causing lower maternal investment (i.e., low levels of maternal licking and grooming; Champagne, 2008). Specifically, through programming of the epigenome and associated biobehavioral changes, low levels of licking and grooming bias development of female pups toward earlier onset of puberty, higher sexual proceptivity toward novel males, increased lordosis in response to male mounts, sharply higher rates of pregnancy following mating sessions, and lower quality parental investment in their own offspring (Cameron, Del Corpo, et al., 2008; Cameron, Shahrokh, et al., 2008; Sakhai, Kriegsfeld, & Francis, 2011). Thus, consistent with psychosocial acceleration theory, female rats growing up under conditions of heightened environmental stress, as indicated by low parental investment in the first week of life, regulate development toward faster life history strategies (Meaney, 2007). Male rats raised under these conditions engage in more play fighting as adolescents (Parent & Meaney, 2008) and aggressive behavior as adults (Menard & Hakvoort, 2007).

#### *Delineating the ecological context*

A substantial limitation of psychosocial acceleration theory is that it adhered to a cumulative stress perspective and did not delineate the content of familial and ecological stress. Beyond cumulative stress, what is really important in the environment that the developing child's brain detects and responds to in relation to the development of life history strategy? To address this question, Ellis et al. (2009) identified, via a within- and between-species analysis, distinct contextual dimensions that account for much of the variation in patterns of development both across *and* within species.

Development of fast life history strategies depends on adequate bioenergetic resources to support growth and development. Once this energetic threshold is crossed, other environmental conditions become salient determinants of life history strategy (Ellis et al., 2009). A fundamental influence on life history strategy is *extrinsic morbidity–mortality*: external sources of disability and death that are relatively insensitive to the adaptive decisions of the organism. When environmental factors cause high levels of extrinsic morbidity–mortality, even prime-age adults suffer relatively high levels of disability and death. Thus, the probability of a child, or his or her parents and grandparents, surviving able bodied until the child reaches adulthood is greatly reduced. Accordingly, life history theory posits that our brains and bodies have been shaped by natural selection to respond (consciously or unconsciously) to cues to extrinsic morbidity–mortality by developing faster life history strategies (e.g., Quinlan, 2007). This hypothesis has been supported by a large empirical literature in humans indicating that children's exposure to such cues (e.g., growing up in poverty, exposures to violence, harsh childrearing practices) shifts resource allocations toward more risky and aggressive behavior, earlier pubertal timing and sexual debut, enhanced early fertility, less stable pair bonding, more offspring, and less parental investment per child (e.g., Ellis, 2004; Ellis et al., 2009; Nettle, 2010; Nettle & Cockerill, 2010; Placek & Quinlan, 2012; Wilson & Daly, 1997).

In addition to extrinsic morbidity–mortality, environmental unpredictability – variation over time and space in the fitness costs and benefits afforded by childhood environments – also regulates development of life history strategies (Ellis et al., 2009). In environments that fluctuate unpredictably (e.g., changing randomly between Conditions A and B, so exposure by parents or their young offspring

to Condition A does not reliably forecast whether offspring will mature into Condition A or B), long-term investment in the development of a slow life history strategy does not optimize fitness; all of the energy invested in the future is wasted if the individual matures into an environment where life expectancy is short. Instead, individuals should detect and respond to signals of environmental unpredictability (e.g., erratic neighborhood conditions, frequent residential changes, fluctuating economic conditions, changes in family composition, stochastic parental behavior) by adopting faster life history strategies.

Because extrinsic morbidity–mortality and unpredictability are distinct, developmental exposures to each of these environmental factors should uniquely contribute to variation in life history strategy (Ellis et al., 2009). Recent analyses of the National Longitudinal Study of Adolescent Health, the National Institute of Child Health and Human Development (NICHD) Study of Early Child Care and Youth Development, and the Minnesota Longitudinal Study of Risk and Adaptation (MLSRA) support this prediction (Belsky, Schlomer, & Ellis, 2012; Simpson, Griskevicius, Kuo, Sung, & Collins, 2012). For example, in the NICHD and MLSRA studies, exposures to environmental unpredictability in the first 5 years of life (i.e., parental changes, residential changes, job changes) uniquely predicted faster life history strategies in adolescence and emerging adulthood, independent of the effects of unpredictability in later childhood and indicators of extrinsic morbidity–mortality. The NICHD analyses specifically targeted females, while the MLSRA analyses included both sexes but did not find significant sex differences in the strength of the reported effects of early unpredictability.

### *The special role of fathers*

Another limitation of psychosocial acceleration theory is that it did not distinguish between the effects of different family members, such as mothers versus fathers, on the development of life history strategies. To address this issue, researchers have elaborated on psychosocial acceleration theory to develop *paternal investment theory* (Draper & Harpending, 1982; Ellis, 2004; Ellis, Schlomer, Tilley, & Butler, 2012; Ellis et al., 2003), which shares the core assumptions of psychosocial acceleration theory but differs in its emphasis on fathers. Specifically, paternal investment theory posits a unique role for father presence–absence and involvement, separate from the more general effects of mothers or social and ecological stress, in the regulation of *daughters'* sexual development. This perspective contrasts with psychosocial acceleration theory, which is agnostic regarding any special role for father presence–absence and involvement.

The evolutionary basis for emphasizing father effects is that: (a) the quality and amount of paternal investment is – and presumably always has been – widely variable across and within human societies; (b) this variation recurrently and uniquely influenced the survival and fitness of children during our evolutionary history (Ellis, Del Giudice, et al., 2012; Geary, 2005b); and (c) this variation provided unique information about local mating systems that daughters use to guide their sexual decision-making and behavior. The mating system is important because more polygynous cultures and subcultures are characterized by heightened male intrasexual competition, dominance-striving, and violence, with concomitant diminution of paternal involvement and investment (Draper & Harpending, 1982, 1988). Paternal investment theory posits that natural selection designed girls' brains to detect and encode information about their fathers' social behavior and role in the family (including potentially olfactory cues; see Ellis, 2004) as a basis for calibrating their own life history strategies, with lower paternal investment regulating female sexual decision-making and behavior toward earlier and faster life history strategies.

The strongest support for paternal investment theory comes from a large body of research showing that girls who grow up without their biological father in the home experience earlier pubertal development (e.g., Alvergne, Faurie, & Raymond, 2008; Webster, Graber, Gesselman, Crosier, & Orozco Schember, 2014), earlier initiation of sexual activity (e.g., Ellis et al., 2003), high rates of teenage pregnancy (e.g., Ellis et al., 2003), increased willingness to engage in risky sexual behaviors (e.g., Ellis, Schlomer, et al., 2012; James et al., 2012), and heightened risk of sexually transmitted infections (Mackey & Coney, 2000) than girls who grow up with their biological fathers in the home. The effects of father absence on daughters' pubertal and sexual outcomes appear to be most pronounced when physical separation occurs early in life (e.g., Ellis et al., 2003), which could reflect both calibration

toward faster life history strategies in daughters and reduced monitoring of daughters' early romantic involvement in father-absent homes (Byrd-Craven, Geary, Vigil, & Hoard, 2007; Flinn, 1988). In addition to the well-established effects of father absence, there is also an emerging literature linking lower quality of father–daughter relationships (e.g., decreased paternal warmth, emotional closeness) to earlier pubertal development and sexual debut and increased sexual risk-taking in daughters (e.g., Ellis, Schlomer, et al., 2012; Vigil & Geary, 2006). Many studies have found that fathers have larger, or unique, effects relative to mothers on daughters' sexual behavior (reviewed in Guilamo-Ramos et al., 2012).

Although research testing predictions from paternal investment theory and other life history models has established replicable effects of family and ecological conditions on development of life history strategies, little of this work has been genetically informative. Quasi-experimental studies in humans have only tested the father presence–absence/paternal investment pathway, with somewhat mixed results (supported a causal effect: D'Onofrio et al., 2006; Ellis, Schlomer, et al., 2012; Tither & Ellis, 2008; did not support a causal effect: Mendle et al., 2009; indeterminate: Mendle et al., 2006). Randomized, longitudinally designed prevention trials afford the best possibility for testing the causal status of current evolutionary–developmental models. Such prevention trials would need to target high-risk families and intervene in early childhood to alleviate ecological adversity (e.g., socioeconomic status) and enhance the quality of parental investment. In the absence of such experimental data, however, one must be cautious about attributing causal status to the observed relations (despite the confirmatory experimental data in rats, as reviewed above).

### *Differential susceptibility*

Although life history theory provides a framework for predicting and explaining environmental effects on the regulation of life history strategies, the effect sizes of family context in predicting pubertal timing as well as adolescents' behavioral adjustment are typically small (e.g., Belsky et al., 2007; Sentse, Veenstra, Lindenberg, Verhulst, & Ormel, 2009) and thus leave much behavioral variability unexplained. A possible explanation for these small effects is that children may be differentially susceptible to their family environments. Several related evolutionary models posit that natural selection has maintained variation in susceptibility to environmental influence (reviewed in Ellis, Boyce, Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2011). *Differential susceptibility* is emerging as an important and generative framework in developmental science for explaining Organism  $\times$  Environment interactions (e.g., Belsky & Pluess, 2009). The core assumptions that define the differential susceptibility framework are articulated in Table 1. This set of guiding assumptions has accrued substantial empirical support (reviewed in Belsky & Pluess, 2009; Ellis, Boyce, et al., 2011).

An important phenotypic indicator of differential susceptibility to environmental influence is *biological sensitivity to context*, which Boyce and Ellis (2005) defined as neurobiological susceptibility to both cost-inflicting and benefit-conferring features of the environment. Neurobiologically-susceptible individuals, according to the theory, are more attuned to environmental signals, for better and for worse. Hence, more susceptible individuals are not only more receptive to supportive environments (such as by detecting positive opportunities and learning to capitalize on them) but also more responsive to dangerous or uncertain environments (e.g., by developing lower thresholds for detecting and acting on perceived threats).

Boyce and Ellis (2005) operationalized biological sensitivity to context as heightened autonomic or adrenocortical reactivity to environmental challenges. These challenges were part of a standardized laboratory protocol in which kindergarteners were exposed to mild stressors across multiple domains (sensory, social, cognitive, and emotional) for the purpose of assessing their parasympathetic nervous system, sympathetic nervous system, and cortisol responsivity. Children who were more biologically reactive to the laboratory stressors (usually modeled at +1 *sd*) were given the shorthand designation of *orchid children*, signifying their special susceptibility to both highly stressful and highly nurturing environments. Children low in reactivity (usually modeled at –1 *sd*), on the other hand, were designated as *dandelion children*, reflecting their relative ability to function adequately in a wide variety of circumstances (Boyce & Ellis, 2005).

The idea of differential susceptibility to the environment, as captured by the distinction between orchid and dandelion children, has far-reaching implications for life history theory—and any other

**Table 1**

Core assumptions of the differential susceptibility paradigm. (From: Ellis, B. J., Boyce, W. T., Belsky, J., Bakermans-Kranenburg, M. J., & van IJzendoorn, M. H. (2011). Differential susceptibility to the environment: An evolutionary–neurodevelopmental theory. *Development and Psychopathology*, 23, 7–28.)

1. Individuals characterized by heightened environmental susceptibility display enhanced sensitivity to *both* negative and positive environments, i.e., to both risk-promoting and development-enhancing environmental conditions
2. This enhanced sensitivity increases *developmental* receptivity to the environment. That is, more susceptible individuals are more likely to experience sustained developmental change, not just transient fluctuations in functioning, in response to environmental exposures
3. Susceptibility to the environment is instantiated in the biology of the nervous system; it is *neurobiological* susceptibility. Genetic susceptibility factors operate through neurobiological processes and behavioral indicators of susceptibility are grounded in neurobiology
4. Developmental experience plays a role, along with heritable polygenic variation, in determining individual differences in neurobiological susceptibility
5. Individuals of all ages—children and adults—vary in neurobiological susceptibility to environmental influences, and, within individuals, susceptibility may vary across the life span
6. Individual differences in neurobiological susceptibility are *adaptive* in the evolutionary sense and have been conserved by fluctuating selective pressures that generate different fitness pay-offs across different social, physical, and historical contexts (or at least did so during the course of human evolution)
7. Variation in neurobiological susceptibility to the environment, therefore, constitutes a central mechanism in the regulation of alternative patterns of human development; specifically, differential susceptibility moderates the effects of environmental exposures on developmental and life outcomes. Ultimately, this means that the development of some individuals, more than others, will be influenced by their experiences and environments (even if these were exactly the same)

theory postulating environmental effects on child developmental outcomes. The most radical implication, as articulated by Belsky (1997), is that the small main effects of family context on life history strategies may overestimate the impact of rearing environments in some children (low susceptibility, more fixed development) and underestimate it in others (high susceptibility, more plastic development).

Ellis, Shirtcliff, Boyce, Deardorff, and Essex (2011) investigated this hypothesis in a longitudinal study of children from preschool to high school, in which biological sensitivity to context was investigated when children were 1st graders. They found that lower-quality parent–child relationships in preschool forecasted faster initial tempo of puberty and earlier pubertal timing, but only among children showing biological sensitivity to context in the form of heightened sympathetic nervous system or adrenocortical reactivity. Thus, it was the combination of high biological sensitivity to context and high family stress that predicted earlier and faster reproductive maturation.

Complementing this work focusing on physiological stress reactivity, other researchers have operationalized differential susceptibility to environmental influence in terms of genetic polymorphisms. The assumption is that neurobiological susceptibility to the environment is instantiated in multiple genetic polymorphisms, neurobiological mechanisms, and behavioral phenotypes. In the first study of its kind to investigate the role of genetic variation in moderating environmental effects on pubertal timing, Manuck, Craig, Flory, Halder, and Ferrell (2011) focused on variation in the estrogen receptor gene *ESR1*. Consistent with past research, women who reported being raised in families characterized by distant interpersonal relationships and high levels of conflict tended to reach menarche earlier than women raised in close families with little discord. However, this effect was moderated by *ESR1* variation. Among women who were homozygous for minor alleles of the two *ESR1* polymorphisms examined in the study, a childhood history of low-quality family relationships ( $-1$  *sd*) was associated with a one year decrease in age of menarche compared with a childhood history of high-quality family relationships ( $+1$  *sd*); no such effect was found among women with other *ESR1* genotypes.

Differential susceptibility research is useful in moving the field beyond debates about genetic versus environmental influences. Individuals who are high in neurobiological susceptibility to the environment appear to be most likely to detect and respond to their developmental contexts, showing *conditional adaptation* to environmental conditions, as per life history theory, whereas others who are low in neurobiological susceptibility appear to be more fixed in their development, or at least relatively unresponsive to normal variation in family conditions, as per behavior genetic models focusing on genetically-regulated alternative phenotypes.



## Adaptations of infancy and childhood: ontogenetic versus deferred

Although natural selection operates at all stages of the life span, it is especially potent in the early years of life. Individuals must first survive infancy and childhood before becoming reproductive adults, and the likelihood of dying before adulthood was great for our ancestors (Volk & Atkinson, 2013). This fact means we must look specifically at adaptations associated with infancy and childhood, rather than focusing solely on adaptations in the reproductive adult. From an evolutionary–developmental perspective, adaptations are not viewed so much as encapsulated modules or Darwinian algorithms, executed step-by-step in response to environmental cues. Rather, consistent with the developmental systems perspective and the concept of evolved probabilistic cognitive mechanisms discussed earlier, adaptations—both in terms of adaptive individual differences and species-typical patterns of behavior—arise from reliable interactions between genes and gene products and individual life experiences in the context of a species' ontogenetic niche. Thus, adaptations have an evolutionary and developmental history.

From a developmental perspective, some distinctions can be made among adaptations. Some evolved characteristics of infants and children were specifically selected to serve an adaptive function at a specific time in development, termed *ontogenetic adaptations* (Bjorklund, 1997; Oppenheim, 1981). In contrast, *deferred adaptations* are those aspects of childhood that were selected, at least in part, for their role in preparing children for adulthood (Hernández Blasi & Bjorklund, 2003). By using the term “deferred adaptation,” we do not mean to suggest any teleological implications, as if adaptations in childhood anticipate adult needs. Rather, such adaptations likely function throughout life, adapting juveniles to their current niche but also to the lives they will likely lead as adults (or would have led in the environment of evolutionary adaptedness). This situation is most apt to occur, we argue, when environmental conditions of the juvenile and adult periods are similar, or even continuous (as social composition would likely be in small groups of hunters and gatherers).

Although we believe it is useful to make the distinction between ontogenetic and deferred adaptations, the distinction is not always clear-cut. For example, whereas some physiological adaptations clearly have a function at one time in development (e.g., the umbilical cord during the prenatal period) but no function later in life (i.e., after birth), such ontogenetic adaptations are less easily identified in the social and cognitive domains. When they are identified, they may in fact have both immediate and deferred benefits. This is also true for deferred adaptations (see discussion to follow). Nevertheless, we believe that the concepts of ontogenetic and deferred adaptations provide valuable heuristics for thinking about how natural selection may have operated at different stages in the life cycle and how children today are prepared by natural selection at different points in their development.

Finally, *conditional adaptations* influence the course of children's development, depending on conditions in their immediate environment. Boyce and Ellis (2005, p. 290) defined conditional adaptations as “evolved mechanisms that detect and respond to specific features of childhood environments – features that have proven reliable over evolutionary time in predicting the nature of the social and physical world into which children will mature – and entrain developmental pathways that reliably matched those features during a species' natural selective history.” We discussed conditional adaptations extensively in the previous section, focusing on factors that influence the attainment of various life history milestones, especially puberty, and thus will not discuss them further here.

### *Ontogenetic adaptations*

Almost half of children in hunter–gatherer societies (the best model for human demographics before the agricultural revolution) die before reaching adulthood (Kaplan & Lancaster, 2003; Volk & Atkinson, 2013). Accordingly, natural selection has maintained various adaptations that serve the specific purpose of helping fetuses, infants, and children survive this intense mortality window. Some of the most obvious are adaptations during the prenatal period, permitting the embryo and fetus to get nourishment in a totally different way than it will after birth. For example, embryonic birds have a yolk sack to nourish them before hatching, and mammals have an umbilical cord to provide nourishment and remove wastes. Once the animal is born, these structures cease to be functional (see

Oppenheim, 1981). These are clear examples of ontogenetic adaptations, features that serve to adapt young organisms to their immediate environments and “disappear” when they are no longer needed.

#### *The benefits of immature sensory systems*

One reason ontogenetic adaptations are more difficult to identify in the social and cognitive domains is because some of these adaptations are seen as inefficient forms of mature behavior and not as potential adaptations to the niche of infancy or childhood (Bjorklund, 1997; Bjorklund & Green, 1992). For example, Turkewitz and Kenny (1982) argued that immature sensory systems serve to reduce the amount of stimulation infants have to deal with, limiting competition between senses for neural resources and permitting them to construct a simplified and comprehensible representation of the world. From this perspective, immature sensory systems are not handicaps that must be overcome, but are adaptive and necessary for proper sensory development and learning. The different sensory systems develop in an invariant order for all vertebrates, with audition developing before vision (Gottlieb, 1971). Perceptual experiences are typically correlated with neural development, so that most animals receive auditory stimulation prior to visual stimulation, and early developing senses (e.g., audition) do not need to “compete” for neurons with later developing senses (e.g., vision). When animals receive species-*atypical* patterns of stimulation, however, it interferes with this choreographed dance between gene-influenced neural maturation and perceptual experience. Substantial evidence in support of this position comes from research mainly with precocial birds showing that stimulation of one sense modality (e.g., vision) earlier than “expected” in development can interfere with functioning in later-developing senses (e.g., audition) (see Lickliter, 1990).

#### *Neonatal imitation*

Another candidate for a social/cognitive ontogenetic adaptation is *neonatal imitation* (Bjorklund, 1987). In this now well-documented phenomenon, infants shortly after birth will match facial behaviors (e.g., mouth opening, tongue protrusions) made by an adult (Meltzoff & Moore, 1977). Meltzoff and Moore proposed that neonatal imitation reflects true selective imitation, qualitatively similar to that seen later in infancy. However, the effect is elusive, in that, for the most studied facial gesture of tongue protrusion, the matching behavior disappears around 2 months (e.g., Abravanel & Sigafos, 1984).

A number of researchers have questioned Meltzoff and Moore’s nativist interpretation, showing that the most frequently assessed gesture of tongue protrusion is elicited by a looming black pen or small ball (Jacobson, 1979), flashing stimuli (Jones, 1996; Legerstee, 1991), or music (Jones, 2006). This caused Jones (2009) to propose that rather than reflecting true imitations, neonatal imitation is a young infant’s response to interesting or arousing stimuli.

Although the proximal mechanism of neonatal imitation may have nothing to do with social learning, it may still have an evolved, distal, function. Several researchers have interpreted neonatal imitation as a transient adaptation to solve specific problems of early infancy. For example, some researchers have proposed that such behavior serves to facilitate social interaction between newborns and their mothers (Bjorklund, 1987; Byrne, 2005). By reflexively matching some facial expressions, neonates may foster social responses in their caretakers, maintaining social interaction at a time when they lack the cortical control to behave intentionally. Byrne (2005) described such matching behavior as *social mirroring*, in which one member of a dyad (the newborn) copies the behavior of the other (the mother) to stay “in tune” with one another, serving to foster and consolidate the social interaction. Such coordination may also be a signal of viability to mothers, similar to that proposed for “healthy” cries (Furlow, 1997). As neurological development progresses and infants gain greater intentional control over their behavior, the near-automatic matching of facial expressions disappears. Consistent with this interpretation, Heimann (1989) demonstrated that neonates who showed higher levels of facial matching had higher quality social interactions with their mothers three months later.

Further support for this position comes from a study in which newborns, who were later shown to be cortically blind, were nonetheless able to visually orient to objects before losing this ability (Dubowitz, Mushin, De-Vries, & Arden, 1986), indicating that early visual processing is done primarily by subcortical regions, unlike the “true” imitation observed in children and adults. Similarly, infants as young as 3 days old display recognition memory for brief durations, with such memory being chiefly

controlled by subcortical structures (Pascalis & de Schonen, 1994), which are soon transferred to cortical circuits (Nagy, 2006). These findings are consistent with the argument that neonatal imitation is unrelated (conceptually or neurologically) to later social-learning abilities, but rather serves to elicit caretaking and resources from parents at a time when infants are unable to intentionally control their own behavior.

### *Infant memory*

Some characteristics of infant memory can be described as ontogenetic adaptations – well suited for the niche of infancy and changing along with the life conditions of the rememberer (Bjorklund & Sellers, 2014; Nelson, 2005; Sellers & Bjorklund, 2014). For example, Nelson (2005) proposed that because of infants' prolonged and nearly complete dependence on adults, they should be especially attentive to recurring events in their social world. According to Nelson, young infants' major cognitive goal is to build up memory representations of the important people, places, and things in their environments, tasks that can be adequately accomplished by implicit memory systems. For example, infants are able to identify their mothers within the first weeks of life on the basis of odor (Macfarlane, 1975), voice (DeCasper & Fifer, 1980), and sight (Walton, Bower, & Bower, 1992). According to Nelson, it is not surprising that an explicit/declarative memory system, characteristic of older children and adults, would be of little use to infants, and that “building in complex cognitive goals, and the mechanisms such as explicit or declarative memory for achieving them, appears burdensome and likely to interfere with the primary requirements of this period of life” (Nelson, 2005, p. 369).

Young infants' memory also seems highly tied to context. For example, Rovee-Collier, Schechter, Shyi, and Shields (1992) showed that 2-month-old infants, who learned that kicking their legs while lying in a crib caused a mobile overhead to move, retained this knowledge 24 h later, but only when the crib liner was the same during both acquisition and testing. Rovee-Collier and Shyi (1992) suggested that this somewhat extreme dependency on context prevents young infants from retrieving memories in “inappropriate” situations. Given infants' poor inhibitory abilities (e.g., Baird et al., 2002; Diamond, 1985; Holmboe, Pasco Fearon, Csibra, & Johnson, 2008), such dependency on context may prevent infants from retrieving previously learned memories (actions) in inappropriate situations.

Infants become less dependent on context for remembering their actions over the course of the first year, accompanied by increased mobility and contact with the physical (and social) environment (Learmonth, Lambert, & Rovee-Collier, 2004; Rovee-Collier & Cuevas, 2009), and this also seems adaptive to developing infants. Although all individuals must be cautious in over-generalizing learned responses, as infants' experiences become more varied, memories acquired in one context can be usefully applied in similar contexts. According to Hartshorn et al. (2004, p. 76), “As the physical world of the developing infant progressively expands and the infant's niche also changes, the behavioral solutions to problems that characterized the relatively static habitat and niche of the younger infant must also change or lose their adaptive utility.”

### *The benefits of cognitive immaturity in childhood*

We have argued previously that young children's cognition is well suited for their particular time in life and is not simply an incomplete version of the adult form (Bjorklund, 1997; Bjorklund & Green, 1992). As such, some aspects of children's immature cognition may not be deficits, as they are usually perceived, but associated with some information-processing benefits and thus candidates for ontogenetic adaptations. For example, Piaget (1955) described preoperational children as being especially *egocentric*, in that they relate all experiences to themselves and have a difficult time taking the perspectives of others. Although usually conceived as a cognitive shortcoming, young children's self-referencing of information may foster their learning and memory of new material. People of all ages tend to remember information better when they relate it to themselves. For example, adults who related a list of adjectives to themselves subsequently remembered more of the words than those who related the adjectives to their fathers or to a famous person (Lord, 1980). Similar results have been reported for preschool children. For instance, in one series of studies (Ross, Anderson, & Campbell, 2011), 3- and 4-year-old children showed better recognition memory for self-referenced items, including a series of actions attributed to a cartoon character given the same name as the child rather than another name,

and “shopping” items owned by the child versus an adult (see also Foley, Ratner, & Gentes, 2010). Other research suggests that *private (egocentric) speech* – or children talking to themselves – may benefit their learning. Vygotsky (1962) argued that such speech serves as a *cognitive self-guidance system* that facilitates learning and goes “underground” as covert verbal speech when children are better able to control their thinking. Support has generally been found for Vygotsky’s position (see Winsler, 2009 for a review).

Another example of immature cognition associated with childhood that may have some adaptive benefits is *overestimation*. Compared to older children and adults, young children are the optimists of the world, believing they have greater physical abilities, better memories, are more skilled at imitating models, are smarter, know more about how things work, and rate themselves as stronger, tougher, and of higher social standing than is actually the case (see Bjorklund, 2007 for a review). Following Bandura’s (1997) theory of the development of self-efficacy, young children’s overly rosy perspective of themselves may foster persistence on tasks where a “wiser” or metacognitively more competent child might quit. If young children knew how poorly they really performed these tasks, their sense of self-efficacy could be damaged and they likely would not be so bold in trying new tasks, nor persistent at tasks they do attempt.

For example, in one study, brighter 3-year-olds overestimated their imitation abilities more than less-bright 3-year-olds did (Bjorklund, Gaultney, & Green, 1993). In other research, kindergarten and first-grade children who overestimated their memory abilities on early trials of a task showed greater subsequent improvement on memory tasks than more accurate children (Shin, Bjorklund, & Beck, 2007). These latter findings are consistent with Bandura’s arguments that children’s overestimation biases foster improvements in their abilities by motivating persistence and promoting self-efficacy.

However, task persistence is not the only way in which overly positive self-evaluations can impact children’s behavior. For example, Lockhart, Chang, and Tyler (2002) proposed that young children express *protective optimism*, believing that physical and psychological traits are more apt to change positively over time than negatively and that people have a good deal of control in changing traits. Given young children’s limited physical and psychological abilities, such optimism leads them to believe that they will eventually become competent, again serving a self-protective function.

### *Deferred adaptations*

If you were to ask people, psychologists included, what childhood was “for,” our guess is that most would say “to prepare them for adulthood.” “The child is the father to man” (and the “mother to woman”). This adult-centric position is not unreasonable, particularly in a slow-developing, big-brained species such as *Homo sapiens* that requires many years to master the technological and social skills of their culture. Here, we provide several examples of candidates for deferred adaptations, some involving sex differences in interests in infants and play styles, and others involving negotiating social hierarchies.

#### *Sex differences as candidates for deferred adaptations*

Sex differences are good candidates for deferred adaptations, in which the different types of experiences of boys and girls prepare them for the life they will lead (or would have led in the environment of evolutionary adaptedness) as adults. For example, girls from cultures across the world show more interest in nurturing babies than boys (see Maestripieri & Pelka, 2002). A similar sex difference is seen in many primates (Maestripieri & Roney, 2006). Given the differential investment that women typically make in their offspring relative to men, experience with infants provides girls with the skills they will need as mothers in the future. In keeping with the “practice” hypothesis, female primates with alloparenting experience have lower first-born mortality rates than primiparous primates mothers without such experience (see Hrdy, 1999).

Play styles also show decided sex differences. Play itself is an important adaptation, providing both immediate and deferred benefits to children and serving as a source of creativity (see Bateson, 1976; Bjorklund, 1997). Many theorists have viewed juvenile’s play as a way in which to learn skills important in adulthood (e.g., Groos, 1898; Vygotsky, 1978). Consequently, play functions in the assembly of

skills and is disassembled when the skill is complete (e.g., Bruner, 1972), termed the *scaffolding view* of play by Bateson (1976). The scaffolding view of play is contrasted with what Bateson (1976) called the *metamorphic view*, in which play is not an incomplete or imperfect version of adult behavior but is beneficial immediately and specialized to the niche of childhood. In this way, play can be considered a specific adjustment to the context of childhood. The scaffolding and metamorphic views of play are not mutually exclusive, and it is likely that play affords both immediate and deferred benefits.

Play is observed in the young of many social mammals, and is in fact characteristic of the juvenile period. In an early review of play in animals, Groos (1898, p. 75) wrote, “animals cannot be said to play because they are young and frolicsome, but rather they have a period of youth in order to play.” Geary (2010), in fact, suggested that fantasy play is an important part of the developing ability to mentally generate social scenarios and rehearse social strategies, and Nielsen (2012) proposed that the pretense and counterfactual thinking involved in fantasy play was, along with imitation, an essential component of childhood and responsible for the emergence of the human mind. According to Nielsen (2012, p. 176), “By pretending children thus develop a capacity to generate and reason with novel suppositions and imaginary scenarios, and in so doing may get to practice the creative process that underpins innovation in adulthood.” There are other types of play, of course, including physical play, especially rough-and-tumble play, and object play, and these too may serve specific functions for children, both immediately and in anticipation of the future. However, despite the importance of play for all children, there are sex differences in styles of play, and these, too, may serve to prepare children for adult life.

With respect to sex difference in play style, perhaps the most obvious is for *rough-and-tumble play* (R&T), which involves chasing and wrestling and often resembles fighting, except it is done with a “play face,” children usually do not get hurt, and they usually do not separate after the bout. Boys engage in more R&T than girls, often in the context of groups and group competition, which afford boys with greater experience cooperating, perhaps enhancing their abilities to better compete against other groups of boys. Some theorists have suggested that R&T, particularly in groups, prepares boys for intrasexual competition (see Geary, 2010; Pellegrini & Smith, 1998). Such play may be especially important for boys in hunter–gatherer societies, preparing them for coalitional hunting and warfare at the group level (Keeley, 1996). Similar sex differences in R&T have been found in other mammals (e.g., Smith, 1982).

There are also sex difference in object play (to be discussed later in this article) and symbolic, or fantasy, play, with the play of girls being more focused on relationships (e.g., playing house, school), whereas the fantasy play of boys tends to emphasize dominance themes – cops and robbers, cowboy and Indians, or superheros versus supervillains, depending on current cultural themes (see Pellegrini, 2013). This pattern is consistent with the roles of men and women in traditional cultures, and likely for our ancestors, with women’s relationships being more intimate, whereas men’s are based more on status.

The sex differences we classify as deferred adaptations reflect a high degree of plasticity, with natural selection providing only initial biases, and often a species-typical supportive environment to produce species-typical adult behavior, at least much of the time. This is true for most psychological adaptations of human infancy and childhood, with natural selection having shaped children’s sensitivity to characteristics of the environment, increasing their ability to adjust to local conditions, survive the early years of life, and develop to become a successful adult in their group.

### *Negotiating social hierarchies*

Children’s play is frequently done in groups. Such groups typically have structure, with different children having different positions in a social hierarchy and/or different roles within the group. Learning how to interact successfully in groups not only provides immediate benefits to children, but also helps them develop the skills they will need for navigating the social environment in adulthood.

One thing important in all human groups is *status*, and through interacting with others, children “learn their place” within that group and acquire skills for navigating social hierarchies in other groups. Structured social groups and differential status are not unique to humans and reflect evolved ways in which social animals organize themselves for purposes of distributing resources related to mating and survival (Hinde, 1976).

Differences in status within a group are often described in terms of *dominance hierarchies*. In most nonhuman social animals, dominance hierarchies reflect “who can beat up whom,” or, in chickens, for instance, what the “pecking order” is, with higher-ranking individuals literally pecking at the heads of individuals lower in the hierarchy. Rather than producing high levels of aggression (e.g., chickens constantly pecking one another), once a dominance hierarchy is established, it serves to reduce aggression and conflict, as individuals know who is likely to win any competitive bout, making physical aggression unnecessary when a potential conflict of interest arises (e.g., who gets first crack at some food item).

As perhaps the most social of all animals, humans also seek status and readily establish dominance, or social, hierarchies, sometimes using the same aversive behaviors seen in other species, but also using other means (e.g., intelligence, leadership ability) to determine one’s rank in an (imperfect) hierarchy. Dominance hierarchies can be observed among groups of preschoolers (e.g., [Hawley & Geldhof, 2012](#)), but are more apparent during middle childhood, mainly because this is the time when children usually begin to spend more unsupervised time in the company of other children. We should note that “dominance” as used in this context reflects interactions among specific individuals, not between all possible group members, in part because in some large groups it is unlikely that all members would interact ([Archer, 1992](#)).

Dominance hierarchies serve to reduce antagonism within the group, distribute scarce resources, and focus division of labor ([Hawley, 1999](#); [Savin-Williams, 1979](#)). For instance, when establishing a group, children use aggression selectively in competing with their peers over resources, toys for example. This is especially true for boys, who engage in more overt, physical aggression than girls, who are more likely to engage in indirect, relational aggression (see [Crick & Grotpeter, 1995](#)). Boys also use high levels of relational aggression, but because of girls’ greater sensitivity to relational aggression, it is a more effective strategy for girls than for boys ([Geary, 2010](#)). Once dominance hierarchies are established, rates of aggression decline (but rarely disappear), and leaders increasingly use prosocial and cooperative strategies to maintain their favorable position in the group ([Hawley, 2003](#); [Pellegrini & Bartini, 2000](#)). Note that from an evolutionary perspective, aggression is not viewed as necessarily maladaptive, the way it is typically perceived by mainstream developmental psychologists (see [Bjorklund & Hawley, 2014](#); [Hawley, 2007](#)). Although aggression among children can lead to serious problems in school and other social settings (e.g., bullying), and children who display high levels of aggression sometimes engage in other antisocial or criminal behaviors, it can be used to gain valuable resources, to defend friends, and generally serve to learn to influence people, and many children who engage in high levels of aggression are psychologically well-adjusted (see [Hawley, Little, & Rodkin, 2007](#)).

Learning to navigate one’s social group has immediate as well as deferred benefits to children. There is also a variety of ways in which children can attain status, which may vary depending on the particular social group in which children find themselves. However, in addition to any immediate benefit maneuvering a social network may afford, it also provides children skills they will use as adults. Moreover, in hunter–gatherer and other traditional communities with stable populations, not only would the skills acquired in youth be useful in adulthood but many of the relationships themselves would be stable. Thus, most if not all deferred adaptations provide children not only with “practice” for later life but also with some immediate benefit.

## Developing domains of mind

A core assumption of mainstream evolutionary psychology is that the human mind/brain evolved not as a powerful, general problem solver, but rather as an organ with multiple domain-specific mechanisms designed by natural selection to deal with specific aspects of the physical or social environment ([Tooby & Cosmides, 1992](#)). Counter to this “massive modularity” viewpoint, in which the brain can be thought of as a Swiss-army knife with many evolved, specialized tools that operate independently ([Tooby & Cosmides, 1992](#)), is the “soft modularity” view ([Geary, 2005a](#); [Geary & Huffman, 2002](#)), which postulates that modules within a domain are organized hierarchically, with lower-level modules, designed to process less-complex information, serving as building blocks for

higher-level, more complex and flexible modules. This permits information processed at lower levels to be integrated, allowing complex skills and cognitions to emerge through experience. Geary's (1995, 2005a) hierarchical model is depicted in Fig. 2.

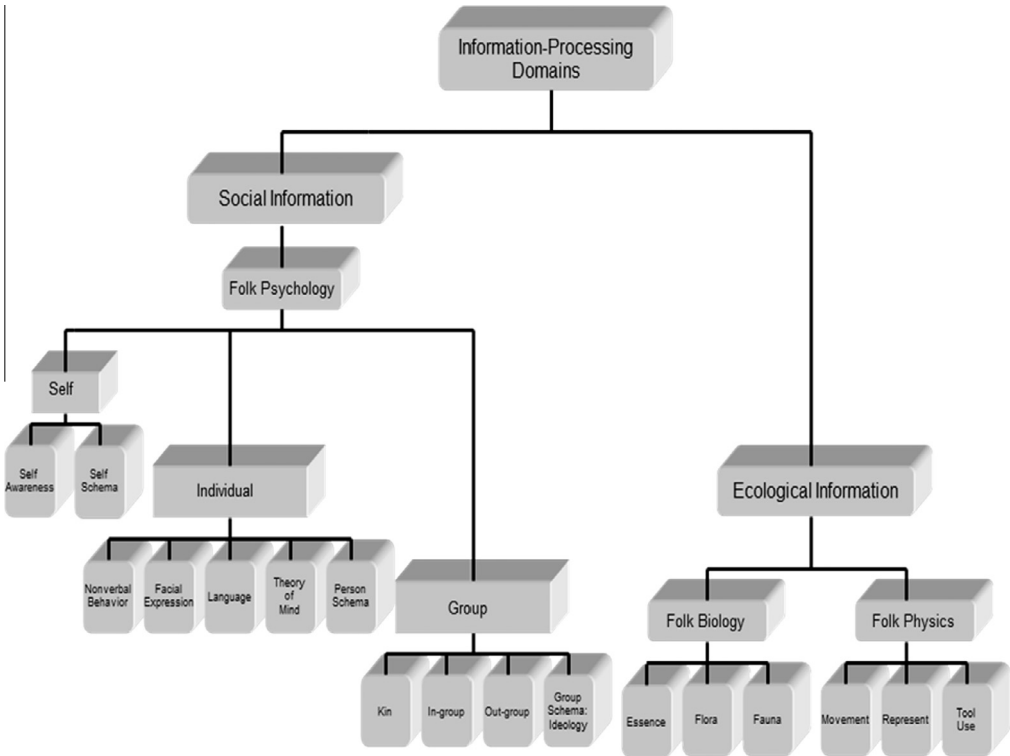
Implicit in an evolutionary approach is that there are *constraints* on learning (Gelman & Williams, 1998; Spelke & Kinzler, 2007). Beginning at birth, infants are more attentive to and able to learn some contents more easily than others. Although children are not born as blank slates, equally able to acquire any information that impinges on their senses, neither are they born with “innate,” or well-developed knowledge sets. Rather, evolutionary–developmental psychologists proposed that infants possess simple biases, or *skeletal competencies* (Geary, 2005a), which are fleshed out over development through exploration, play, and social engagement. This theoretical camp is sometimes referred to as *neonativists* (Baillargeon, 2008; Carey, 2011; Spelke & Kinzler, 2007), arguing that infants possess *core knowledge* that permits them to acquire information about some aspects of the world (e.g., the nature of physical objects) quickly and efficiently. According to Gelman and Williams (1998, p. 600), “From an evolutionary perspective, learning cannot be a process of arbitrary and completely flexible knowledge acquisition. In core domains, learning processes are the means to functionally defined ends: acquiring and storing the particular sorts of relevant information which are necessary for solving particular problems.”

Other scientists, proponents of “hard” developmental systems theory, argue that a core-knowledge approach ignores the role of experience in the formation of these early information-processing biases (e.g., Spencer et al., 2009). As adherents of developmental systems perspectives ourselves, we are sympathetic to these latter arguments; however, we do not believe that the research findings of the neonativists are contradictory to those of developmental systems theorists. As we pointed out earlier in this article, we believe that all adaptations, regardless of when they appear, have their roots in earlier experiences, shaped by the bidirectional interaction between all levels of an organism and its environment (both *macroenvironments*, such as the family and one's culture, and *microenvironments*, such as neurotransmitters and chemicals affecting the functioning of DNA molecules). Language counts, and we will strive to avoid the impression of early perceptual or cognitive biases as being “innate”; nonetheless, we will present evidence that infants are prepared to make sense of some forms of stimulation more readily than others, and that such processing biases have been shaped by natural selection (some of which are also found in other species); but, as we stressed earlier, “prepared is not preformed.”

In this section, we look at the development of several proposed skeletal competencies following Geary's model. From the realm of folk psychology (peoples' intuitive understanding of themselves and other people) we examine the development of intentionality and social learning in infants and young children, and from the realm of folk physics (peoples' intuitive understanding of the physical world) we explore the development of object representation and tool use. To illustrate the significance and possible phylogeny of some of these proposed evolved abilities, they are sometimes contrasted with the comparable abilities in humans' genetic relatives, the great apes (mostly chimpanzees), with whom we last shared a common ancestor between 5 and 7 million years ago.

### *The development of folk psychology*

A large and plastic brain afforded early humans (as well as contemporary people) the possibility to acquire complex technology (see Kaplan et al., 2000), but also the ability to establish “societies” far more complicated than those found in other primate species, and, once established, for children to learn the complexity of those societies. According to the *social brain hypothesis*, the formation of complex human social groups created selection pressures for primates to meet the daily challenges of cooperation and competition among other intelligent group members (e.g., Alexander, 1989; Dunbar, 2003; Hare, 2011). Charles Darwin (1871) recognized the significance of humans' enhanced sociality writing “It serves notice that as soon as the progenitors of man became social . . . the advancement of the intellectual facilities will have been aided and modified in an important manner, of which we see only traces in the lower animals. . .” (p. 161). In fact, even if “big brains” are necessary for acquiring the sophisticated technology associated with all human cultures, the transmission of such skills is most readily accomplished via humans' exceptional social-learning abilities (e.g., Horner,



**Fig. 2.** Geary proposed that the mind is hierarchically organized into domains, with lower-level modules, designed to process less-complex information, serving as building blocks for higher-level, more complex and flexible modules. Within the social domain of folk psychology, domains are further organized into those dealing with self-knowledge, dealing with individuals, and dealing with groups. Within the ecological domain, Geary proposes two subdomains, one dealing with the biological world and the other the physical world. *Source:* Geary, D. C. (2005). *The origin of mind: Evolution of brain, cognition, and general intelligence*. Washington, DC: American Psychological Association.

Whiten, Flynn, & de Waal, 2006; Whiten & Flynn, 2010), permitting the nongenetic transmission of acquired information from one generation to the next with high fidelity. Bjorklund and Bering (2003) argued that a large brain, an extended period of immaturity, and social complexity interacted synergistically over hominin evolution, with large brains and an extended juvenile period being necessary for mastering the ways of one's group, and social complexity in turn exerting selection pressures for increased brain size and an extension of the pre-adult life span. Consistent with this contention, Joffe (1997) compared the size of the nonvisual neocortex with the length of the pre-reproductive period and size of the social group for 27 primates, including humans, and reported that the proportion of the life span spent as a juvenile was positively correlated with group size and the relative size of the nonvisual neocortex.

#### *Social responsivity in young infants*

As all mammals, human infants are highly dependent upon their mothers and other caregivers immediately after birth. Until the advent of prepared foods, all the nutrition a young infant received came directly from its mother. Given the extreme dependence of human infants, it behooves them to establish strong and positive relationships with their significant others. Natural selection has prepared them to do just that, and to do it in some ways that are seemingly unique in the animal kingdom, afforded by our species' enhanced folk-psychology abilities. Research from a variety of sources indicates that even neonates have a tendency to orient toward social stimuli. This social orientation



in newborns is seen in their attention to biological motion (e.g., Bardi, Regolin, & Simion, 2014) and to faces (e.g., Mondloch et al., 1999), especially eyes (Gava, Valenza, Turati, & de Schonen, 2008). Moreover, their use of cries, coos, and smiles to attract adult attention, and their matching of facial expressions (e.g., Meltzoff & Moore, 1977), all serve to promote strong bonds between themselves and their caregivers (usually the mother), which not only keep them safe and alive immediately, but also serve as the basis of subsequent social relationships (see Simpson & Belsky, 2008; Thompson, 2006). Support for the importance of infants' early social responsivity comes from studies showing that infants who are sickly and are slower to display typical signs of sociality (e.g., social smiles, eye contact, cooing) are more likely to be subsequent victims of abuse (e.g., Martin, Breezley, Conway, & Kempe, 1974; Sherrod, O'Connor, Vietze, & Altemeier, 1984). Moreover, the absence of certain social-cognitive abilities in some children, despite normal general intelligence (e.g., children with autism spectrum disorder), is consistent with the argument that human social intelligence is not simply derivative of our species' general cognitive abilities but rather represents dedicated, evolved abilities.

Of course, children are also socialized to be social – encouraged to share, empathize, and cooperate with other people – and much about social behavior must be learned through experience. Philosophers and evolutionary biologists have long pondered the issue of altruism in *H. sapiens*, questioning how seemingly selfless behavior could have been selected over the course of evolution and whether it is an inherent feature of human nature or learned through the prompting of others (see Warneken, 2013). A modern evolutionary perspective does not claim that sociality is innate, but rather proposes that infants and young children have perceptual and affective biases that orient them to social stimuli and relations, promoting the development of sociality. These behaviors develop early, before parents specifically instruct children in cultural norms of “proper” behavior. In fact, many researchers point out that adults in traditional societies rarely directly instruct their children (Lancy & Grove, 2010). Rather, children acquire social and technical skills primarily by observing older peers and adults, often during routine activities and communication of everyday life, which Rogoff (2003) termed *guided participation*. Some of these adaptations may be unique to humans, while others are shared, at least in rudimentary form, with other great apes.

#### *Viewing others as intentional agents*

Although infants' attention to and understanding of other people improve over the early months of life, human social interaction requires, at its most basic, the ability to view other people as *intentional agents* – individuals who *cause* things to happen and whose behavior is designed to achieve some goal (see Bandura, 2006). Despite young infants' social orientation and considerable social skill in manipulating their parents, they seem not to treat others as intentional agents until the latter part of the first year (see Tomasello, 2009; Tomasello & Carpenter, 2007). Early evidence of this is in the form of *shared attention*, sometimes referred to as *joint attention* (e.g., see Carpenter, Akhtar, & Tomasello, 1998; Tomasello & Carpenter, 2007), which involves a triadic interaction between the infant, another person, and an object. This is easily seen during parent–infant interaction, with parents pointing out objects to infants (referential communication). Other researchers have suggested that intentionality develops even earlier in infancy when measures other than shared attention are used (e.g., Csibra, 2008; Kovács, Téglás, & Endress, 2010). For example, Kovács et al. (2010) reported that 7-month-old infants looked longer at an animated event in which an actor's expectation was violated (a ball was not behind an occluder where the actor expected it would be) than in a baseline condition.

Shared-attention abilities improve over the next year (see Tomasello, Carpenter, & Liszkowski, 2007). For instance, 10-month-old, but not 9-month-old, infants have an understanding of social gaze, expecting conversation partners to look at one another (Beier & Spelke, 2012), and 12-month-olds will point to objects to inform others about events they do not know (Liszkowski, Carpenter, & Tomasello, 2007). Between 12 and 18 months, infants will use another person's gaze to direct their own attention (Brooks & Meltzoff, 2002) and will point to objects to direct an adult's attention to something he or she is searching for (Liszkowski, Carpenter, Striano, & Tomasello, 2006). Beginning around 12 months, infants engage in social referencing, using a parent's facial expression, tone of voice, gestures, or combinations of these sources to determine their actions in an uncertain situation, such as how to react to an unfamiliar adult (e.g., Hornik, Risenhoover, & Gunnar, 1987; Vaish & Striano, 2004).

Being able to share a perceptual experience hardly seems like a task of great cognitive complexity or consequence, but it is one that is seemingly not possessed by great apes. For example, although chimpanzees and some monkeys will follow another's gaze in some situations (Bering & Povinelli, 2003; Bräuer, Call, & Tomasello, 2005) and point out things to others (Leavens, Hopkins, & Bard, 2005), most researchers argue there is no evidence of shared attention in mother-reared great apes (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Russell, Mauthner, Sharpe, & Tidswell, 1991; Tomasello & Carpenter, 2005; but see Leavens et al., 2005). An exception seems to be for referential pointing in enculturated apes, apes raised much as children are, in which at least one member of each great-ape species has been found to engage in referential pointing (see Bjorklund, Causey, & Periss, 2010 for a review).

There is even debate about whether chimpanzees understand that “seeing is knowing.” For example, when chimpanzees sat in front of two human caretakers – one with eyes visible and the other with eyes occluded – with a desired food item between them, they made begging gestures indiscriminately, suggesting an ignorance of the role of seeing (and eyes) in “knowing” (Povinelli & Eddy, 1996). Other research, however, indicates that chimpanzees in a food-competition scenario with a conspecific do understand that being able to see something implies knowledge: a subordinate chimp would only retrieve a food item when it was out of the visual field of a more dominate chimp (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001; see also Melis, Call, & Tomasello, 2006). However, this rudimentary ability, which would seem to be a necessary precursor for shared attention, appears to be limited to food competition in chimpanzees and not used across social settings, as it is in human children. This ability to extend cognitive skills to other contexts may be a general difference between humans and other species. The seemingly sophisticated abilities of other species are often limited to specific contexts and do not generalize beyond them (Penn, Holyoak, & Povinelli, 2008).

### *Social learning*

Infants' and young children's strong social orientation make it highly likely that important cultural lessons will be learned in interaction with other people, making *social learning* a particularly powerful mechanism for acquiring information. At its most general, social learning can be defined as occurring in a situation “in which one individual comes to behave similarly to another” (Boesch & Tomasello, 1998, p. 598). The primary mechanism of social learning in children 2 years of age and younger appears to be *emulation*, in which they recognize the goal of a model but do not necessarily copy the exact behaviors to achieve that goal (e.g., Nielsen, 2006). This is contrasted with “true” imitation in which the learner identifies the model's goal and uses the same behaviors as the model to achieve this goal (Tomasello, 2000).

Beginning usually sometime during the third year of life, children's social-learning strategy changes. Now they will copy all actions of a model, even those that are irrelevant to attaining the goal (e.g., Lyons, Young, & Keil, 2007; Nielsen, 2006), termed *overimitation*. For example, in one study, preschool children watched as an adult performed a series of actions to open an object to get a toy locked inside. Children copied both relevant and irrelevant actions to open a box, even after being warned to avoid “silly,” unnecessary actions (Lyons et al., 2007).

Preschool children are not necessarily imitating blindly, however. For example, preschool children were less likely to imitate a model when they had just solved an easy versus a more difficult task, presumably because those with an easy experience had discovered relevant affordances on their own, whereas children with a difficult prior experience had not needed assistance from the model (Williamson, Meltzoff, & Markman, 2008). Preschool children also imitate selectively when they know the specific goal of a task beforehand (Williamson & Markman, 2006), when they have information about an object's causal structure across multiple trials (Schulz, Hoopell, & Jenkins, 2008), or when they have some awareness of the specific intentions of the model (Gardiner, 2014; Gardiner, Grief, & Bjorklund, 2011). Despite the contextual nature of overimitation, its prevalence during the preschool years, and its persistence into adulthood in some contexts (e.g., McGuigan, Makinson, & Whiten, 2011), is compelling and counterintuitive, and a number of researchers believe that it reflects an evolved adaptation.

For example, Whiten, McGuigan, Marshall-Pescini, and Hopper (2009) proposed that overimitation reflects an evolved heuristic for learning about cultural artifacts and their uses. Unlike other species,

human children must learn about thousands of artifacts, all cultural inventions, and a parsimonious way in which to acquire such knowledge is to copy exactly modeled behaviors with respect to the artifacts. In the process, some irrelevant actions may be acquired, but these can be “weeded out” via individual learning. Consistent with this, children seem to think that modeled actions on objects are normative. For example, 3- to 5-year olds corrected a puppet that omitted unnecessary actions previously performed by an adult, protesting that the puppet was “doing it wrong” (Kenward, 2012; see also Keupp, Behne, & Rakoczy, 2013). Similarly, Gergely and Csibra (2005; Csibra & Gergely, 2011) argue that children’s indiscriminate imitation is a human adaptation permitting fast and accurate transmission of information between individuals, which they refer to as *natural pedagogy*.

Chimpanzees and bonobos also display substantial levels of social learning (see Whiten, 2010), yet such learning is clearly different in both quantity and quality from that shown by human preschool children. For example, when shown how to use a tool to retrieve out-of-reach food, chimpanzees will fail to copy irrelevant actions of a model if there is a more efficient means of achieving the goal (e.g., Horner & Whiten, 2005; Nagell, Olguin, & Tomasello, 1993), displaying emulation rather than imitation. There is also no evidence of overimitation in chimpanzees (see Nielsen, 2012), seemingly because chimpanzees seem not to distinguish between intentional versus accidental actions as well as human children do.

An exception to this pattern is reported for enculturated apes, raised much as human children are. Several researchers have reported that human-reared apes display true imitation both immediately after a demonstration (e.g., Buttelmann, Carpenter, Call, & Tomasello, 2007; Carrasco, Posada, & Colell, 2009; Tomasello, Savage-Rumbaugh, & Kruger, 1993) and following a significant delay (e.g., Bering, Bjorklund, & Ragan, 2000; Bjorklund, Yungler, Bering, & Ragan, 2002; Tomasello, Kruger, & Ratner, 1993). These findings indicate that a species-atypical rearing environment for infant chimpanzees resulted in a species-atypical pattern of cognitive development, one more similar in some ways to a pattern shown by human children (Bjorklund & Rosenberg, 2005; Call & Tomasello, 1996). These findings suggest that humans’ common ancestor with chimpanzees also likely possessed the rudiments for cognitively advanced social learning and the plasticity required to modify their ontogenetic trajectory in response to changed environmental conditions (Bjorklund, 2006).

Social-cognitive development follows a species-typical path in all cultures, reflecting the importance of a social orientation for human infants and children. For example, although the responsiveness of the caregiver influences infants’ shared attention (e.g., Deák, Walden, Yale Kaiser, & Lewis, 2008; Goldsmith & Rogoff, 1997), shared attention is highly canalized and is expressed similarly in diverse cultures (e.g., Callaghan et al., 2011). With respect to social learning, overimitation is not limited to children from Western cultures but has been observed in 2- to 6-year-old Kalahari Bushman children (Nielsen & Tomaselli, 2010). Human thought, social interaction, and culture itself is almost unimaginable without the cognitive intersubjectivity characteristic (perhaps uniquely so) of our species.

Yet, although human societies share much in common, there is also great cultural and environmental diversity, and this requires a plastic cognitive system. Infants’ and children’s social biases only orient them to social stimuli, permit them to share perceptual experiences, and to transmit information between individuals; they do not provide children with “content,” for example, which faces to be most attentive to, what normative rules to follow, or to whom to pay special attention. Moreover, individual differences in children’s rearing experiences have been shown to influence myriad aspects of children’s social cognition, including shared attention, empathy, social learning, and theory of mind (see Bjorklund et al., 2010). Cultural and sex differences are also consistently reported for theory of mind (e.g., Shahaeian, Nielsen, Peterson, & Slaughter, 2014; Wellman, Fang, Liu, Zhu, & Liu, 2006), which extend into adulthood. For instance, Chinese adults consistently outperformed American adults in perspective-taking tasks (Wu & Keysar, 2007). Thus, folk psychology involves highly canalized biases that orient infants and children to important social stimuli. These are “skeletal” abilities (Geary, 2005a), however, that are fleshed out by more flexible social-cognitive mechanisms, permitting children to adapt to a broad range of social and physical environment.

### *The development of folk physics*

Although developing an understanding of the social world seems especially important to human children, children, like the young of all animals, must also acquire an understanding of the physical

world. Much of Piaget's research was devoted to how children developed an understanding of "physics" (e.g., the permanence of objects, conservation). Piaget proposed a universal developmental trajectory of what Geary (2005a) refers to as folk physics, and contemporary psychologists have attempted to use an evolutionary lens to view the development of some of these abilities. In this section, we examine briefly the development of object representation over infancy, abilities that seemingly all mammals eventually develop, followed by a look at the development of tool use, which, although not unique to humans, is most fully developed in *H. sapiens*.

### *Object representation*

The laws of Newtonian physics operate constantly and consistently, causing anyone over 2 years old to take them for granted. Yet, infants must learn that objects fall when not supported (and fall down, not up), that an object does not change size or shape depending on how one views it (*object constancy*), that individual objects are seen as cohesive wholes with distinct boundaries (*object continuity and cohesion*), and that objects continue to exist out of one's perception (*object permanence*). According to some researchers, infants attain quickly an understanding of these properties of objects, facilitated by processing biases, many of which they share with other animals.

Perhaps the most basic form of object knowledge is object constancy. For example, when newborns are habituated to an object at one distance from their eyes and then shown one of two new objects – one the same object but seen from a different distance, and the other a new object of a different size but presented so that the retinal image it projects is the same as the retinal image projected by the original habituated object – they continue to habituate to the same object/different distance, even though the actual retinal image is different (Slater, Mattock, & Brown, 1990).

In other research, infants as young as 2 months of age behave as if they understand that objects are continuous in nature. For example, in one series of experiments, infants were habituated to a rod protruding both above and below a box and later looked longer when shown the rod in two pieces than when shown the complete rod, suggesting that the babies inferred that a complete rod was previously present behind the obstructing box (e.g., Johnson & Aslin, 1995). In other research, 2.5-month old infants watched as a toy mouse moved behind one screen on the far right of a display then reappeared seconds later from behind a screen on the far left side of the display without moving across the empty middle portion (Aguiar & Baillargeon, 1999). Infants looked longer at this display than when the mouse travelled across the screen, causing the authors to propose that these young infants understood that objects must traverse a continuous path in getting from point A to point B. Other research, using violation-of-expectation procedures in which infants look longer at unexpected than expected events, has shown that 2.5 month olds understand the concept of collision (e.g., Kotovsky & Baillargeon, 1994, 2000; Wang, Kaufman, & Baillargeon, 2003). Some other notions of object continuity and cohesion develop a bit later. For example, research by Baillargeon and her colleagues has shown that it is not until about 4.5 months of age that infants understand that an object must have contact with a platform lest it fall, and 6.5 months before they realize that the object will fall unless a significant portion of it is in contact with the platform (Baillargeon, Kotovsky, & Needham, 1995; for other examples, see Aslin, 2007; Baillargeon, 2008). Perhaps we should not be too surprised of these accomplishment by young infants, for such basic knowledge of the properties of objects is possessed by most, if not all land mammals (see Hauser, 2000).

With respect to the most-studied form of object knowledge in infancy, object permanence, research by Baillargeon (1987; Baillargeon & De Vos, 1991), using the violation-of-expectation procedure, demonstrated that infants as young as 3.5 months old understand that objects continue to exist when out of their sight, nearly 5 months earlier than Piaget (1954) observed infants able to retrieve a completely hidden object. Although not all nonhuman mammals pass more advanced forms of object-permanence tasks (e.g., invisible displacement), all mammals tested are able to recover a hidden object (Dore & Dumas, 1987). What is impressive about human infants is that they display this knowledge, via their looking behavior, months before they can demonstrate it by searching.

Taken together, research performed from the nativist perspective has been interpreted as reflecting infants' possession of impoverished notions of objects at birth that get fleshed out with experience over the first year of life (see Baillargeon, 2008; Spelke & Kinzler, 2007). For example, based on these and other findings, Baillargeon (2008, p. 3) proposed that infants are born with the *principle of*

*persistence*: “objects not only exist continuously and remain cohesive, they also retain their individual properties. According to this principle, no object can undergo a spontaneous or uncaused change in the course of an event.” Infants are initially biased to attend to only some violations of persistence, but with experience their representations are enriched and they will demonstrate sensitivity to a broader range of violations of persistence.

The core-knowledge perspective has been criticized as unnecessarily postulating innate knowledge when the phenomena under study can be more parsimoniously explained by lower-level perceptual processes (see e.g., Clearfield & Mix, 1999; Clearfield & Westfahl, 2006; Hood, 2004; Spencer et al., 2009). For example, in a much cited (and replicated) study, Wynn (1992) showed that 5-month-old infants were sensitive to changes in the number of objects that were placed or removed from behind a screen, and she interpreted these results as infants possessing a rudimentary notion of addition and subtraction. Other researchers, however, have shown that infants may not be responding to *number*, and thus performing primitive (and unconscious) addition and subtraction; rather, they are responding to the total amount of *substance* present (Clearfield & Westfahl, 2006; Mix, Huttenlocher, & Levine, 2002), suggesting that decisions are based more on perceptual than conceptual relations (Uller, Carey, Huntley-Fenner, & Klatt, 1999; see Mandler, 2000). Although such an interpretation may be counter to the view that infants are born with, or develop early, modular-like cognitive adaptations (i.e., “innate” knowledge), they are consistent with our perspective that adaptive behaviors develop as a result of inherited perceptual and information-processing biases in interaction with a species-typical environment, i.e., evolved probabilistic cognitive mechanisms following a “soft” developmental systems theory perspective.

#### *Learning to use tools*

Humans may not be the only species to use and make tools, but it is inarguable that our species’ ability in this domain is magnitudes greater than that of any other animal. In fact, tool manufacture and use was once a defining characteristic of humans, as reflected by paleoanthropologists’ name for the earliest discovered member of our genus, *Homo habilis* (handy man). Tool use does not seem to be only a reflection of humans’ greater general intelligence, but to have some adaptations specific to learning to use tools, and some of these can be seen in infancy and early childhood.

Human infants and children are seemingly drawn to explore and interact with objects, which several researchers have proposed serves to help them discover *affordances* of objects (functional relationships between objects and the environment) and how objects can be used as *tools* (Bjorklund & Gardiner, 2011; Geary, 2005a; Smith, 2005). Smith (1982, p. 151) argued that object exploration and play may help prepare children to use tools “over and above what could be learnt through observation, imitation, and goal-directed practice.” *Exploration* involves gaining information about an object by manipulating it, possibly with visual inspection (Belsky & Most, 1981; Hutt, 1966), whereas object play is usually defined as the active manipulation of objects, such as banging them and throwing them, but also as the use of objects to build something (Bjorklund & Gardiner, 2011). Although it is often difficult to differentiate between exploration and object play, most interaction with objects before 9 months of age is usually considered exploration, with most such interaction following about 12 months being described as play (Belsky & Most, 1981). Preschool children devote about 10–15% of all behaviors to object play (Smith & Connolly, 1980). Object play is typically low in frequency during the early preschool years, peaks in childhood, and declines in early adolescence (see Pellegrini, 2013), with similar developmental patterns being found for children from hunter-gatherer and other traditional cultures (e.g., Bakeman, Adamson, Konner, & Barr, 1990; Bock, 2005; Sigman et al., 1988).

There is a sex difference in both exploration and object play, with boys engaging in both activities more than girls (e.g., Bornstein, Haynes, O’Reilly, & Painter, 1996; Caldera, Huston, & O’Brien, 1989). In one study, 3-year-old boys engaged in more object play than 3-year-old girls and performed better than girls on a subsequent simple lure-retrieval task in which children had to select and use the proper tool to retrieve a desired toy. Moreover, the amount of object play predicted success on the tool-use task, but only for boys (Gredlein & Bjorklund, 2005): the correlation between object play and tool-use scores was significant for boys (.59), but not for girls (.04), causing Gredlein and Bjorklund (2005, p. 227) to suggest that “boys may be more sensitive to such environmental experiences than girls,

and that some gender-related factors (e.g., prenatal hormone exposure) other than amount of object play contribute significantly to the observed differences in tool use.” These findings are consistent with the position that sex differences in early behavior interact with skeletal but still-developing folk-physics systems, producing differential behavioral competencies in males and females (Geary, 2005a, 2010).

Children learn early that tools are “special” objects. For example, in one study, 12- and 18-month-old infants watched as an adult inserted the handle of a spoon or novel tool with a spoon-like structure through a small hole in the side of a box to activate a light display (Barrett, Davis, & Needham, 2007). When given a chance to use these tools to turn on the light, the infants were more likely to grasp the bowl end of the novel tool than the spoon. Seemingly, infants’ experience with spoons led them to be less flexible when it needed to be used in an atypical way. “Spoons are grasped by the handle, not the bowl end.” This is an example of the *design stance*, the assumption that tools are designed for a specific purpose. As a result, selecting tools becomes very efficient, although it sometimes results in “functional fixedness,” the tendency not to identify alternative uses for familiar objects (German & Johnson, 2002). The design stance is well documented in adults and is readily seen in preschool children after only a brief introduction to a new tool. For example, 3-year-old children believe that an object designed for one purpose (e.g., catching bugs) is indeed a “bug catcher” even though it can be successfully used for another function (collecting raindrops) (e.g., Bloom & Markson, 1998; German & Johnson, 2002).

The biases that children have for learning to use tools are not independent of their social-learning biases. Although infants and children can learn to use tools by manipulating objects and discovering an object’s properties and affordances as a tool, they are more apt to learn to use a tool by watching more-experienced others interacting and sometimes specifically demonstrating them. For example, in one study, 2- and 3-year-old children either watched as an adult demonstrated how to extract a toy from an apparatus with a tool, had specific haptic (i.e., “hands on”) experience with the tools, or some combination of the two (Gardiner, Bjorklund, Greif, & Gray, 2012). Children learned about the tools better through observation than by manual exploration. The authors argued that, “Evolutionarily, learning tool use through observation would have been selected over modes of independent learning for the efficient and accurate transmission of crucial, adaptive tool-use knowledge” (p. 252).

Object play and tool use have been examined in nonhuman primates. In their review of research on object play in nonhuman primates, Ramsey and McGrew (2005) reported that species that use tools frequently in the wild (chimpanzees) display higher levels of object play than species that use tools less frequently (gorillas), consistent with the proposal that object play serves a role in subsequent tool use and was selected over the course of evolution for that purpose.

With respect to tool use, chimpanzees have been shown to make tools (e.g., stripping leaves off a twig so it can be used to “fish” for termites) and to use a variety of tools, depending on the specific ecological conditions. Such tool use is specific to a particular troop, is transmitted from one generation to another (e.g., Whiten et al., 1999), and for some tasks such as termite fishing and cracking nuts, often take years to master (Carvalho, Biro, McGrew, & Matsuzawa, 2009; Humle, Snowdon, & Matsuzawa, 2009). Although many primate researchers believe that tool use in chimpanzees is achieved through object play (see Ramsey & McGrew, 2005), there is some evidence that tool use is transmitted through social learning, perhaps even teaching (Boesch, 1991; Greenfield, Maynard, Boehm, & Schmidting, 2000). For example, Boesch (1991) reported that mother chimpanzees made exaggerated movements while cracking nuts in the presence of their offspring, suggestive of teaching, and Lonsdorf (2006) reported that the amount of time mothers spent alone or with maternal family members (which is highly correlated with time spent termite fishing) was related to their offspring’s skill at specific components of termite fishing.

Evidence of object play, tool use, and its transmission across generations in chimpanzees, clearly suggests that these abilities were likely possessed by humans’ common ancestor with chimpanzees and provided the foundation upon which a human-like tool-using ability could develop. One major phylogenetic acquisition related to tool use, seen in human children but not chimpanzees, is the design stance. For example, unlike 14-month-old children, chimpanzees, bonobos, and gorillas (but not orangutans) were no more likely to use a tool that a model freely chose to use to solve a task rather than a tool she was required to use (Buttelmann, Carpenter, Call, & Tomasello, 2008). This is likely

related to the apes' lesser-developed social-cognitive skills. Unlike human children, the apes fail to see another individual as an intentional agent, making learning to use tools from observing others less likely than for children.

### **Evolutionary theory: a metatheory for developmental psychology**

As we noted earlier, despite having historical roots within the discipline, developmental psychologists have been slow to embrace evolutionary thinking. One reason is the perception of genetic determinism. If evolution is defined in terms of changes in gene frequencies in populations and genes are seen as the driver of ontogeny, then an application of Darwinian principles to children would seem to leave little room for the influence of family and culture on the development of adult phenotypes and the ability to alter developmental pathways in ameliorative ways. However, as an increasing number of developmentalists are realizing, this is an inaccurate view of evolution. Natural selection has shaped humans to be sensitive to environmental contingencies early in life, providing flexibility in the routes individuals take to adulthood in order to increase their inclusive fitness. Perhaps one of the most important features of *H. sapiens* that has evolved over the eons is cognitive and behavioral plasticity, afforded in large part by our species' extended period of immaturity. Thus, change and the ability to adapt to varied environments are not only the bread and butter of many developmental psychologists, but also the features selected over the course of human phylogeny.

As we stated in the opening pages of this article, we see an evolutionary perspective as a metatheory for developmental psychology. It provides a consilient, overarching perspective, integrating distal and proximal causes of behavior and cognition. With respect to development, important influences occur on different time scales, and these must be integrated in order to provide a proper picture of development. There are a host of proximal causes of development, of course, from the firing of neurons to schedules of reinforcement. Regardless of the specific focus of a researcher, changes over development must be explained in a model that considers the interaction between a child and all levels of his or her environment. Variants of developmental systems theory, discussed earlier in this paper, provide such a model, and the bidirectional interaction between a biologically endowed child and his or her environment is a foundational assumption of evolutionary–developmental psychology. Natural selection may have shaped the genomes of our ancestors, but genes are always expressed in a context, and such contexts serve as the proximal causes or mediators of development.

One especially important context for humans is the social environment. At one time, the Standard Social Science Model dominated thinking in the social sciences and denied any significant biological influence (including evolutionary accounts) on important human behaviors (Tooby & Cosmides, 1992). However, as the content of much of this paper shows, modern evolutionary theory recognizes the centrality of the social environment for human development. Humans are inherently social creatures – shaped by natural selection to cooperate and compete with conspecifics, and they are prepared to learn to do so over the course of development. Human culture is as much a part of human nature as our upright stance or opposable thumb. To attempt to examine or explain human development independent of culture is a fool's errand. Children have been reared within social groups with specific traditions and values ever since there have been humans. The institutions, tools of intellectual adaptation (Vygotsky, 1962), and values of a culture vary substantially between human groups, and children have evolved the cognitive skills to be sensitive to the cues of others in their environment and to be able to extract the information needed to adapt to their particular social milieu. Far from being incompatible with a sociocultural perspective, an evolutionary account of development recognizes that children's evolved cognitive mechanisms have been shaped to function in species-typical environments, and for *H. sapiens* that means not only a womb and lactating mother, but also a social context.

Although controversies about evolutionary approaches to development remain (e.g., Spencer et al., 2009), evolutionary ideas have invaded mainstream thinking in developmental psychology. Moreover, we argue that not only should an evolutionary approach be the core for developmentalists, but a developmental approach should be the core of any evolutionary theory. Perhaps the central idea of an evolutionary approach to development is that natural selection has operated at all periods of the life span, although not necessarily equally. Selection will have its greatest effects on early stages of

development: getting born, developing to sexual maturity, finding a mate, and rearing offspring to reproductive age. Any benefits that encourage development through these stages will be favored, even if they have negative effects later on. Moreover, how infants and children adapt to conditions early in life determines to a significant degree how they will function as adults.

Theodosius Dobzhansky (1973) famously said, “nothing in biology makes sense except in the light of evolution.” We make the same argument for psychology, particularly for the understanding of infants, children, adolescents, and their development.

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