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Early stress, parental motivation, and reproductive decision-making: applications of life history theory to parental behavior

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Abstract

This review focuses on the impact of parental behavior on child development, as interpreted from an evolutionary-developmental perspective. We employ psychosocial acceleration theory to reinterpret the effects of variation in parental investment and involvement on child development, arguing that these effects have been structured by natural selection to match the developing child to current and expected future environments. Over time, an individual's development, physiology, and behavior are organized in a coordinated manner (as instantiated in 'life history strategies') that facilitates survival and reproductive success under different conditions. We review evidence to suggest that parental behavior (1) is strategic and contingent on environmental opportunities and constraints and (2) influences child life history strategies across behavioral, cognitive, and physiological domains.

Introduction

The determinants of child behavior are multi-faceted and complex. Here we focus on the effects of parental behavior on child development, and we present evolutionary-developmental models of how these effects vary within and between households. Models of child development that are not explicitly informed by evolutionary theory are often agnostic to functional or ultimate interpretations of behavior. Applying an evolutionary framework to the effects of parental behavior on child development allows us to examine these effects as potential *adaptive responses* (whether conscious or unconscious) to ecological constraints and opportunities. From this perspective, value labels derived from WEIRD ideals (Western, Educated, Industrialized, Rich, and Democratic [1]) on what is 'good' or 'bad' parenting are not useful [2,3]. Rather, the value of different parenting styles is relative and contingent on the environment in which the individual resides (regardless of ideals about parenting). Well-intentioned interventions designed to reduce 'problematic' behaviors tend to be based on WEIRD values that may be mismatched to high-adversity contexts and strip individuals of

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the very tools and behaviors that facilitate success in such contexts (as in 'declawing the cat' [4]).

The present review expands on current work by synthesizing evolutionary-developmental research and emphasizing the integrative nature of this approach. Our review is broken down into three main sections: (a) brief primer of a foundational evolutionary model of human social development (psychosocial acceleration theory), (b) evaluation of psychosocial acceleration theory in terms of major tests and theoretical extensions, and (c) implications for future research.

Psychosocial acceleration theory: a primer

The major strengths of applying Darwinian thinking toward parenting and development are twofold: First, it integrates and organizes proximal-level theories and their findings (*e.g.*, social learning theory, attachment theory, *etc.*) into a cohesive framework. Second, it reframes variation in parenting and child development as strategies that were shaped by natural selection to maximize survival and reproduction under different environmental conditions. Taken together, these contributions facilitate generation of novel hypotheses and reinterpretation of existing literature.

Belsky *et al.* [2] integrated traditional developmental theories, such as attachment theory and social learning theory, with life history theory [5,6] to advance an evolutionary model of child socialization – *psychosocial acceleration theory* – which substantially influenced subsequent evolutionarily-oriented models of social development. Figure 1 outlines the ontogenetic pathways and key developmental domains posited by Belsky *et al.* [2] and extended by follow-up research and theory.

Psychosocial acceleration theory posits that the first five to seven years of a child's life, when attachment to a primary caregiver is labile, is a sensitive time to gauge the predictability and accessibility of resources present in the environment, the level of cooperation and mutualism between individuals, and the durability and stability of romantic relationships. Children who reside in high-stress households characterized by poor access to resources and increased psychosocial stressors will be more likely to orient development in a manner that prioritizes reproductive output over investment in health and stable pair bonds, producing a cascade of downstream effects on psychological, physiological, reproductive, and health domains. These tradeoffs, which begin during prenatal development and continue over the life course, constitute intra-individual calibrations across physiology, morphology, brain and behavior.

Over time, these tradeoffs generate an organized constellation of traits and behaviors known as *life history strategies.* Life history strategies reside on a continuum from slow to fast, whereby fast life history strategists prioritize investment in mating, emphasizing offspring quantity (see Figure 1). Slow life history strategists conversely prioritize investment in somatic maintenance and parentalnepotistic effort, emphasizing offspring quality. Differential investment between these facets of development is guided by both heritable [7] and ecological forces [2,8]. As Belsky *et al.* [2] emphasized, the model should be

conceptualized less as a series of sequential pathways and more as a 'cumulative-conditional-probability' model (p. 650). This means greater or lesser exposure to harsh conditions that are detected and encoded by the child will increase the probability that their development will be oriented toward a particular end of the life history continuum [8] (as shown in Figure 1).

Important tests and extensions of psychosocial acceleration theory

A central prediction of psychosocial acceleration theory is that ecological cues to adult *extrinsic morbidity-mortality* (which is defined as the probability of disability or death resulting from external sources that are relatively insensitive to the organism's resource-allocation decisions [8]) should orient individuals to pursue faster life history strategies (*e.g.*, [8,9••]). Psychosocial acceleration theory emphasizes that parenting and household contexts provide important cues to the child about levels of extrinsic morbidity-mortality in the larger ecology. Conflictual households denoted by low-quality parenting such as neglect, abuse, low parental monitoring, or father absence indicate to the developing child that the immediate environment is harsh, unpredictable, and uncontrollable and that the individuals residing in it may not be trustworthy or cooperative (see Refs. [10,11]). These household and family cues are hypothesized to regulate development toward prioritizing reproduction over parenting and health-maintaining behaviors. The result is a faster life history strategy, emanating from lifetime developmental trade-offs, spanning across many domains (as shown in Figure 1). Here we briefly review how these processes shape worldviews and cognitions, calibrate peripheral neuroendocrine systems, and regulate sexual development.

In harsh and unpredictable environments, individuals should have highly developed *unpredictability schemas*: a worldview where other people and future outcomes are perceived as unreliable and unpredictable (see Figure 1: Psychological/Behavioral Development). Household and family-level unpredictability is often defined in terms of variability in the ecology of the family (*e.g.*, moving residences and schools, changes in caregivers and/or parental relationships [12–14]). Work focusing on the unpredictability schema has found a link between these family-level indicators of unpredictability and increased perception of unpredictability [15•,16]. Growing up under such household conditions should orient individuals to prioritize mating effort over parental obligations and impact the development of children. Consistent with this view, research examining low-income mothers and their elementary school children found that both decreased parental effort and increased mating effort were associated with a more highly developed child unpredictability schema [15•]. Retrospective examination of family unpredictability designated by inconsistency in discipline/nurturance, family meals, and income was associated with a more developed unpredictability schema in college students [16]. Further, the association between family unpredictability and anxious-depressive symptomology was mediated by the unpredictability schema, suggesting that maintaining a hypervigilant and uncertain worldview of the ecology and conspecifics may impact mental health as measured by standard instruments. From an evolutionary perspective the development of vigilance in an unpredictable environment is presumed to be an adaptive response because individuals displaying that trait in that context are likely to avoid fitness-damaging outcomes (compared with non-vigilant individuals in the same context), even if being in a vigilant psychological

state translates into anxious-depressive symptoms. As shown in Figure 1, parental condition (*e.g.*, mental and physical health; marital stability) is part of the family and ecological context of the child, which shapes quality of parental investment and, through it, child developmental outcomes such as emerging life history strategies. Longitudinal analyses found that maternal depression in early childhood (predicted by lower socioeconomic status and greater household unpredictability in terms of parental and residential changes) was associated with increased household chaos, more parental hassles, harsher parenting at ages 4–5 years old, and earlier onset of sexual activity [12,17]. Moreover, other research has shown that exposure to unpredictable conditions in early childhood can impact an individual's approach toward parenting, decreasing supportive parenting mostly in men [18••].

Psychosocial acceleration theory [2] focused on the role of familial and ecological conditions in regulating the development of life history strategies. The Adaptive Calibration Model (ACM [19,20•]) has attempted to extend psychosocial acceleration theory by articulating physiological mediators – autonomic, neuroendocrine, metabolic, and immune – that instantiate these proposed environmental effects (see Figure 1: Autonomic, Adrenocortical, and Immune Signaling). In the ACM, activation of these physiological mediators during childhood provides crucial information about threats and opportunities in the environment, their type, and their severity. Over time, this information becomes embedded in the parameters – recurring set points and reactivity patterns – of autonomic, neuroendocrine, metabolic, and immune systems. These parameters provide the developing person with statistical 'summaries' of key dimensions of the environment. For example, sustained activation of the HPA axis is generated by exposures to danger, unpredictable or uncontrollable contexts, and social evaluation, as well as energetic stress (see Refs. [21,22]); thus, the HPA axis tracks the key environmental variables involved in regulation of alternative life history strategies. Immune system parameters also track critical dimensions of environmental stress and support [23,24]. In turn, individual differences in biological stress responses regulate the coordinated development of a broad cluster of life history-relevant traits [19,20•]. Stress response systems further coordinate across other physiological systems (*e.g.*, the gonadal axis) to regulate sexual maturation and reproduction [9••,19,25–27].

Sexual maturation is a precursor to reproduction. As shown in Figure 1, environments characterized by increased harshness and unpredictability can be expected to shorten childhood and accelerate reproduction to maximize fitness opportunities. Research indeed suggests that increased childhood adversity predicts earlier pubertal timing and accelerated sexual behavior and reproduction [28,29,30•,31–38]; reviewed in Ref. [36]. These psychosocial effects on sexual development and reproduction may, importantly, be moderated by attachment styles. In a landmark study, secure infant attachment to mothers acted as a buffer against environmental harshness (as measured by income-to-needs ratio during the first five years of the child's life): Insecurely attached girls residing in harsher environments went through puberty earlier, but the association was not found for securely attached girls [30•]. This moderating effect underscores the key role of parent-child relationships in regulating the development of life history strategies.

Implications for future research

Evolutionary developmental psychology has proven to be a productive field in terms of generating novel hypotheses and lines of research across both evolutionary and developmental domains. Many of the pathways shown in Figure 1 are now well established. We must now move beyond establishing associations and focus on examining the underlying genomic and physiological mechanisms. One area that has received much attention is mother-child relationships and the regulation of gene expression. Foundational animal models, which have used a 'cross-fostering' paradigm to control for genetic and environmental confounds (reviewed in Ref. [39]) have shown that high-quality parenting (indexed by high levels of licking and grooming in rodents) down-regulates autonomic and adrenocortical stress reactivity. This calibration of stress responsivity presumably prepares the developing pup for a relatively safe, stable environment. This calibration is instantiated mechanistically through methylation of glucocorticoid receptors in hippocampal neurons [39]. Human parallels have begun to be studied. Exposure to prenatal or early life stress in the form of maternal depressive symptoms during pregnancy or early childhood maltreatment predicts methylation of human glucocorticoid receptors in the cord blood (of newborns) or buccal cell (of infants), which in turn has been associated with important child outcomes such as internalizing behaviors at 3–5 years [40–42]. This type of epigenetic research has the potential to shed great light on how life history strategies are instantiated under different conditions and how it may impact future health and longevity [43,44].

Another important direction for future research will be examining how and if different life history strategies are actually adaptive in context. Life history theory moves us beyond value judgments about 'good' or 'bad' parenting and instead emphasizes adaptation in context. From a life history perspective, the child growing up under harsh, unpredictable conditions who develops insecure attachments, an exploitive interpersonal style, matures early, sustains early sexual debut, and engages in a range of antagonistic and risky social behaviors is no less functional than a child who grows up in a safe, stable environment and shows the opposite behaviors and dispositions. For example, Humphreys *et al.* [45] provides experimental evidence showing that previously institutionalized children pursue exploitative strategies in a decision-making context, resulting in greater success in a restricted task condition in which it paid off to 'cash in' early. These data suggest that developmentally-calibrated exploitive strategies may be adaptive in unpredictable environments where future outcomes are uncertain. Research is needed to examine the specific skills and abilities that develop in response to stressful rearing environments (see Ref. [46]) and how these skills can be usefully employed in relevant contexts. An example is heightened attention-shifting ability among individuals who grow up in harsh, unpredictable home environments and then are exposed to current states of economic decline and uncertainty [47••]. Heightened attention-shifting ability may facilitate vigilance in a world where threats come without warning.

Finally, we have discussed linkages across cognition, stress reactivity, and sexual maturation. These systems should be investigated in concert and continued to be examined in context [48], consistent with physiologically-oriented models of development [26,46,49]. Evolutionary-developmental models emphasize linkages across varying levels of experience

and development ranging from familial and ecological stress to psychological/behavioral development to neurobiological mechanisms to reproductive strategies to health (see Figure 1). While this multi-level integration may not happen overnight, such a change would require modification of training programs in human development, emphasizing not only culture and context, but genetics, biology, and evolutionary thought, as well. Proposing these paradigm shifts within these academic spaces may be met with resistance [50].

In conclusion, psychosocial acceleration theory has served as an important foundation and stimulus for evolutionary-developmental work on parenting and its role in regulating life history strategy. The perspective has proven useful in integrating across multiple domains of analysis, highlighting the importance of previously understudied variables (*e.g.*, mortality cues, timing of puberty, time perspective), and placing parenting in a coherent, integrative framework that is functionally organized around variation in life history strategies in relation to ecological context.

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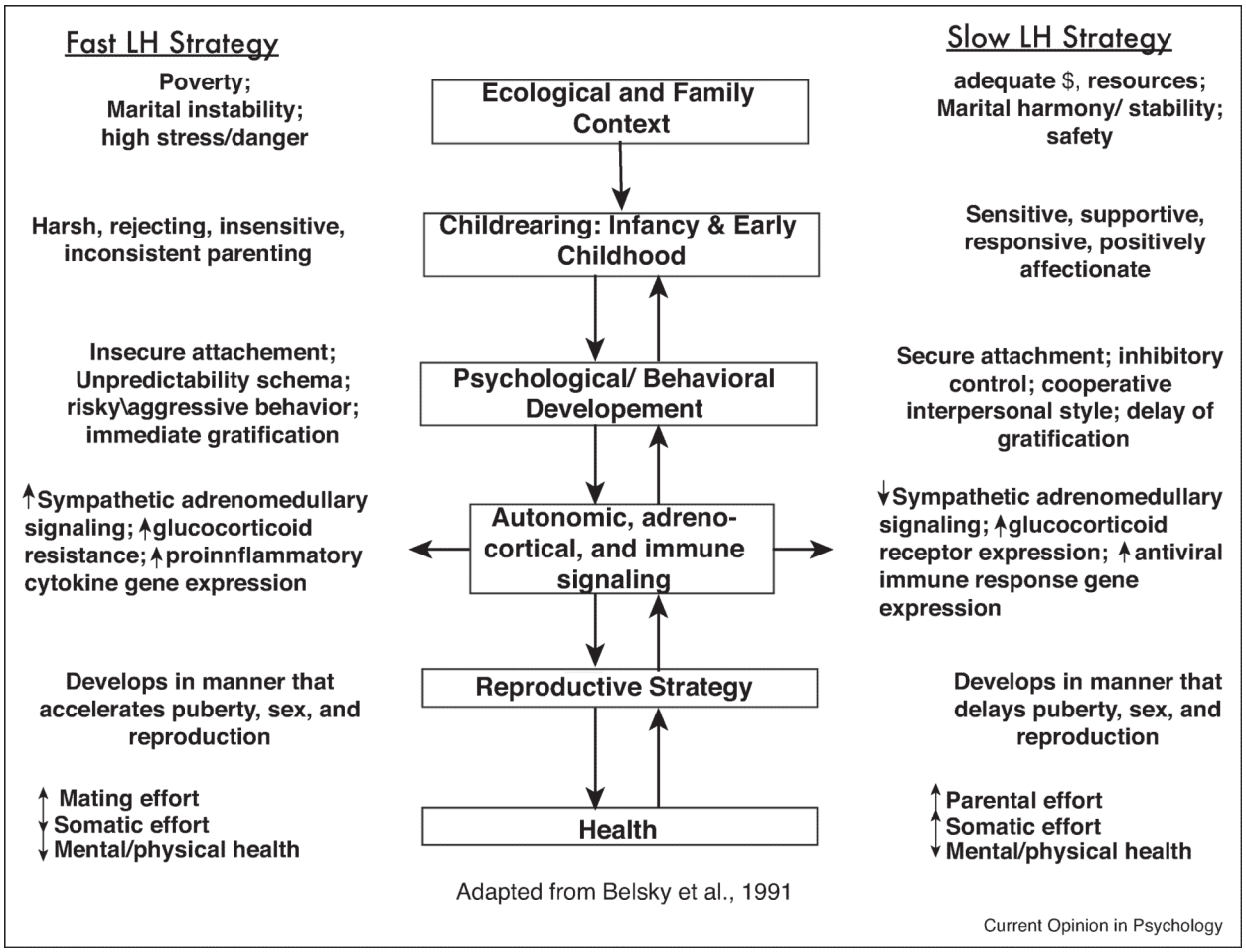

Figure 1.

A modified figure of the Psychosocial Acceleration Theory, originally proposed by Belsky et al. [2] and extended in subsequent work. The figure posits that early childhood experiences (first 5–7 years old) will orient a child's development in a manner that is creates a cohesive life history strategy. Life history strategies reside on a fast-slow continuum whereby individuals oriented toward a faster life history strategy will emphasize reproduction over health-maintenance and high-quality parenting; conversely, individuals oriented toward a slower life history strategy will emphasize investment in health-maintenance and high-quality parenting. Although Psychosocial Acceleration Theory emphasizes environmental causation, the bidirectional arrows highlight the importance of child effects and bidirectional causation more generally. The horizontal arrows indicate that autonomic, adrenocortical, and immune signaling also operate as important moderators of the proposed pathways.