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Beyond Risk and Protective Factors:

An Adaptation-Based Approach to Resilience

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Abstract

How does repeated or chronic childhood adversity shape social and cognitive abilities? According to the prevailing *deficit model*, children from high-stress backgrounds are at risk for impairments in learning and behavior, and the intervention goal is to prevent, reduce, or repair the damage. Missing from this deficit approach is an attempt to leverage the unique strengths and abilities that develop in response to high-stress environments. Evolutionary-developmental models emphasize the coherent, functional changes that occur in response to stress over the lifecourse. Research in birds, rodents, and humans suggests that developmental exposures to stress can improve forms of attention, perception, learning, memory, and problem-solving that are ecologically relevant in harsh-unpredictable environments (as per the *specialization hypothesis*). Many of these skills and abilities, moreover, are primarily manifest in currently stressful contexts where they would provide the greatest fitness-relevant advantages (as per the *sensitization hypothesis*). These theory and data support an alternative adaptation-based approach to resilience that converges on a central question: "What are the attention, learning, memory, problem-solving, and decision-making strategies that are promoted by exposures to childhood adversity?" At an applied level, this approach focuses on how we can work with, rather than against, these strengths to promote better intervention outcomes.

Keywords: adaptation, animal behavior, cognitive abilities, developmental plasticity, early-life stress, evolutionary-developmental psychology, intervention, life history theory, phenotypic plasticity, resilience

Introduction

Many children and youth from disadvantaged communities do not eat, sleep, live, work, or go to school in safe, stable places. It is now well known that growing up under such stressful conditions undermines health, development, and learning (e.g., Duncan et al., 2010; Farah et al., 2006; Shonkoff et al., 2012). This knowledge has powerfully influenced how scientists and policy makers view at-risk populations; indeed, it has helped form the foundation of the prevailing *deficit model* of development under stress, which emphasizes "what's wrong with the kids" who come from harsh, unpredictable environments. Although the deficit model takes different forms (e.g., *cumulative risk*: Evans et al., 2013; Sameroff et al., 1987; Seifer et al., 1996; *toxic stress*: Shonkoff et al., 2012; and *allostatic load*: Lupien et al., 2006; McEwen & Stellar, 1993), the common emphasis on impairments in learning and behavior has painted a bleak picture of at-risk populations, as exemplified by recent *Science* articles titled "Poverty impedes cognitive function" and "The poor's poor mental power" (Mani, Mullainathan, Shafir, & Zhao, 2013; Vohs, 2013). Implicit in the deficit approach is the assumption that children and youth from high-risk backgrounds are broken and need to be fixed (e.g., made better at sustaining attention, delaying gratification, and following rules—to help them think and act more like children and youth from low-risk backgrounds).

In this paper, we argue that the deficit model is incomplete because it misses how individuals adapt to their environments by fine-tuning their cognitive abilities to solve recurrent problems faced in their local ecologies. We propose an alternative strength-based approach that asks: "What's right with these kids?" Although we do not question the assumption that early-life stress undermines certain cognitive abilities, we believe that this is only half of the story. The other half is that individuals who develop in harsh, unpredictable environments specialize their cognitive abilities to match high-adversity contexts (Ellis & Del Giudice, 2014; Frankenhuis & de Weerth, 2013; Mittal et al., 2015), and that these abilities can be used to enhance intervention outcomes and resilience.

To meaningfully represent this other half of the story, we refer to individuals who grow up under high-adversity conditions as "stress-adapted" (rather than "vulnerable" or "at-risk"). In advancing this adaptation-based approach to resilience, we conceptualize *cognitive abilities* broadly to include both social and cognitive skills for which performance can be evaluated against objective (i.e., agreed upon) benchmarks such as speed or accuracy. This focus on objective benchmarks distinguishes the current adaptation-based approach from previous approaches emphasizing *posttraumatic growth* (which involves "positive change experienced as a result of the struggle with trauma" in goals, beliefs, priorities, and related interpersonal processes; Meyerson, Grant, Carter & Kilmer, 2011, p. 949; see also Janoff-Bulman, 1989).

Throughout this paper, we use the term "adaptive" in the evolutionary sense, as referring to fitness outcomes (survival and reproduction), and not in the clinical or public health sense, as referring to health, safety, or psychological well-being. Theory and research in evolutionary biology has come to acknowledge that, in most species, single "best" strategies for survival and reproduction are unlikely to evolve. This is because the best strategy varies as a function of the physical, economic, and social parameters of one's environment (Crawford & Anderson, 1989), and thus a strategy that promotes success in some environmental contexts may lead to failure in others. Selection pressures therefore tend to favor *phenotypic plasticity*, the capacity of a single genotype to support a range of phenotypes in response to ecological conditions that recurrently influenced fitness during a species' evolutionary history (e.g., Pigliucci, 2001; West-Eberhard, 2003). Herein we use the term *adaptive* in reference to such phenotypically plastic developmental responses (i.e., *conditional adaptations*; Boyce & Ellis, 2005), focusing on the development of specialized skills and abilities in response to harsh, unpredictable environments. We hypothesize that these skills and abilities are conditional adaptations that were shaped by natural selection to enhance survival and reproductive success under such adverse conditions.

Because few of the studies reviewed herein actually measure fitness outcomes, our focus will be on the *proposed* function of skills and abilities that are enhanced through developmental exposures to stress. For example, we will describe the development of elevated vigilance in a dangerous environment as 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 it is unpleasant and physiologically costly to be in a vigilant psychological state.

The Specialization and Sensitization Hypotheses

Drawing on an evolutionary-developmental framework, we propose the **specialization hypothesis**: harsh, unpredictable environments do not exclusively impair cognitive abilities; instead, individuals become developmentally adapted ("specialized" and potentially enhanced) for solving problems that are ecologically relevant in such environments (Frankenhuis & de Weerth, 2013). For example, in rapidly changing environments, heightened attention-shifting may enable individuals to take advantage of fleeting opportunities, even if frequent shifting interferes with sustained attention (see Mittal et al., 2015). To improve intervention outcomes in stress-adapted children and youth, we need to uncover a high-resolution map of specific cognitive abilities that are enhanced as a result of growing up in high-risk environments. That would enable design of interventions that work with, instead of against, these abilities.

A corollary of the specialization hypothesis is the **sensitization hypothesis**: the hypothesized advantages in cognitive function among people who grow up under stressful conditions (as per the specialization hypothesis) are manifested primarily under currently stressful conditions (i.e., earlier-life experiences *sensitize* later responses to stress). For example, stress-adapted youth may be advantaged at attention shifting under conditions of current stress and uncertainty, but not in benign, non-threatening circumstances (Mittal et al., 2015).

The sensitization hypothesis assumes that the day-to-day experiences and circumstances of stress-adapted individuals are qualitatively different from those of individuals from low-risk backgrounds and, therefore, that testing stress-adapted children and youth under standard laboratory conditions may disadvantage them by not allowing them to show their abilities in context (i.e., their abilities to solve problems and achieve goals within their local ecology). Stress-adapted children and youth may instead perform certain tasks better in settings that do not attempt to minimize the reality of daily stressors and uncertainties. This could include contexts that expressly highlight the prevalence of daily stressors (e.g., reminders that we live in a world where resources are uncertain) or environments in which people in a room are allowed to move and talk, which may simulate the contexts in which stress-adapted individuals developed their skills. In total, the sensitization hypothesis necessitates studying Test Performance-by-Environment interactions. It involves testing for skills and abilities under different conditions (i.e., experimental manipulations of psychological or environmental states[1]). Gaining knowledge

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[1] The sensitization hypothesis involves experimental manipulations of feelings or motives that are typical of the experiences of children and youth growing up under high-stress conditions (e.g., Mittal et al., 2015). This is different than simply exposing individuals to generally stressful or distracting conditions. To the extent that laboratory manipulations simply increase distraction levels, everyone will show diminished performance.

about environmental conditions that are promotive versus harmful to the performance of stress-adapted children and youth is critical to designing interventions that work with this population.

Focusing a theoretical and empirical lens on how early exposures to harsh, unpredictable environments *adaptively* influence cognitive abilities is critical for understanding how individuals developing in such contexts learn, remember, solve problems, and make decisions. An extraordinarily large body of research has documented the maladaptive consequences of early life stress. This raises the question: Why should knowledge about the cognitive strengths of children and youth who are adapted to harsh, unpredictable environments (of which we know so little) be any less useful than knowledge about their impairments (of which we know so much)? The better we understand cognitive adaptations to harsh, unpredictable environments, including specialization and sensitization effects, the more effectively we can tailor education, policy, and interventions to fit the needs and potentials of stress-adapted children and youth. This adaptation-based approach to resilience exemplifies using psychology to improve people's lives because it illuminates the unique strengths and abilities that develop in response to high-stress environments—and how to use those attributes to enhance learning and developmental outcomes in stress-adapted individuals.

Overview

We begin by reviewing the well-established negative effects of psychosocial adversity on cognitive development, and then summarize how this issue has been conceptualized and addressed in the resilience literature. We then present the theoretical background for an alternative *adaptation-based approach to resilience* that is based in life history theory. To explicate this new perspective, we discuss and evaluate the specialization and sensitization hypotheses through a review of relevant theoretical and empirical literatures, focusing on cognitive adaptations to chronic or repeated childhood adversity in birds, rodents, and humans. We conclude by discussing the implications of the adaptation-based approach to resilience for intervention and propose future directions aimed at increasing research efforts and knowledge in this area of multidisciplinary inquiry.

The Effects of Adversity on Cognitive and Academic Outcomes

The physical, material, and social hardships of poverty encompass a wide range of contexts that may negatively affect child cognitive development and achievement. These contexts include neighborhood danger; exposure to environmental chemicals; bad housing conditions characterized by noise, crowding, and violence; neglectful and abusive parenting; parental mental and physical health problems; family instability resulting in disrupted relationships with caregivers; residential instability; low-quality childcare; and peer and school violence (e.g., Blair & Raver, 2012a; Bradley & Corwin, 2002; Duncan & Brooks-Gunn, 2000). Herein we refer to children and youth experiencing the diverse hardships of poverty as growing up in “high-risk” or “harsh, unpredictable” environments[2] (and thus being stress-adapted).

One of the most robust findings in the field of human development is the pervasive negative effect of poverty on cognitive, learning, and achievement outcomes (e.g., Bradley & Corwyn, 2002; Conger & Donnellan, 2007; Duncan, Magnuson, Kalil, & Ziol-Guest, 2012; McLoyd, 1998). Lower levels of language skill and vocabulary are apparent as early as 18 months in poor children, and lower levels of reading and math skills are evident in kindergarten,

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[2] From an evolutionary-developmental perspective, such environments are considered *harsh* because lower socioeconomic status is linearly related to higher levels of virtually all forms of morbidity and mortality (e.g., Adler, Boyce, Chesney, Folkman, & Syme, 1993; Chen, Matthews, & Boyce, 2002) and *unpredictable* because poverty is systematically linked to greater familial and ecological instability (Belsky, Schlomer, & Ellis, 2012; Raver et al., 2015). Evolutionary models conceptualize harshness and unpredictability as fundamental dimensions of environmental risk (Ellis et al., 2009).

with these discrepancies tending to get worse over time (Fernald, Marchman, & Weisleder, 2013; Mulligan, Hastedt, & McCarroll, 2012). Low family income is a strong and consistent predictor of reduced executive-function abilities (Blair et al., 2011; Evans & Schamberg, 2009), learning disabilities involving reading, writing and mathematics, and overall lower scores on standard intelligence tests and scholastic tests (Heberle & Carter, 2015). Children from impoverished backgrounds are also at an elevated risk for grade repetition, expulsion and suspension from school, and school dropout (Ross et al., 2012).

Extant theory and research has focused on understanding how the diverse hardships of poverty lead to such poor developmental outcomes. A common approach has been to count risk factors in a child's life. Consistent with cumulative risk models of development (e.g., Evans, Li, & Whipple, 2013; Sameroff, Seifer, Barocas, Zax, & Greenspan, 1987; Seifer et al., 1996), this approach involves compositing multiple sources of stress in family environments or examining the additive effects of multiple stressors. The underlying hypothesis in this approach is that the more stressors children are exposed to, the more their developmental competencies will be compromised.

A more fine-grained version of the cumulative risk approach involves testing mediation models, which focus on intervening mechanisms in the relations between childhood stress and subsequent neurobiological and cognitive outcomes. Much of this work focuses on the mediating roles of parental condition and functioning (e.g., depression, low marital quality) and the resulting quality of caregiving (e.g., harsh discipline, low parental sensitivity) in explaining the effects of poverty on child development (e.g., Conger & Conger, 2002; Belsky, Steinberg, & Draper, 1991). Some models seek to identify intervening biological mechanisms, such as patterns of child stress physiology (e.g., Blair & Raver, 2012b; Del Giudice, Ellis, & Shirtcliff,

2011) or the structure and function of key brain areas such as the prefrontal cortex, amygdala, and hippocampus (e.g., Karatoreos & McEwen, 2013). Cumulative risk models have commonly been framed in terms of diathesis-stress, where exposures to childhood adversities interact with personal vulnerabilities (e.g., difficult temperament, heightened biological reactivity to stress, low-activity MAOA allele) to predict child developmental outcomes. In the diathesis-stress framework, certain children or youth are vulnerable or resilient because of personal characteristics that moderate environmental risk.

However the theoretical pie is sliced, these approaches attempt to account for deficits in learning and behavior. Children from high-adversity backgrounds are considered to be at risk for impaired development, and these models attempt to explain the causes, mediators, and moderators of that impairment.

The Traditional Strength-Based Approach to Resilience

Despite the overall low achievement levels of children and youth from socioeconomically disadvantaged backgrounds, there is striking variation in the outcomes of individuals exposed to high adversity. Some of these individuals thrive, or at least "beat the odds", despite their high-risk background. This observation has led to a resilience literature that has pushed back against cumulative risk approaches and instead has focused on developmental assets, emphasizing the importance of positive resources and promotive factors that enable children and youth to overcome their challenging life circumstances.

Much is now known about the factors associated with resilient outcomes in young people. As reviewed by Masten (2001, 2014), major predictors of resilient outcomes in youth from high-risk environments include such *individual factors* as intelligence and problem-solving skills, hope and optimism, self-control, planfulness, and motivation to succeed; such *relationship* *factors* as effective caregiving and parenting quality, close relationships with capable adults, and close friends and romantic partners; and larger *social system factors* that provide resources and protection such as effective schools and communities. These established resilience factors have provided the foundation for interventions that focus on promoting resilience. In total, the resilience literature asks “What does it takes to succeed?” and “How can we build these strengths and qualities in children and youth?”

Resilience Metaphors

This approach to resilience has led to a set of intervention strategies that share the common goal of helping children to compensate for weaknesses or otherwise overcome developmental histories of stress and adversity. Several metaphors are useful in describing the specific goals of traditional resilience interventions. We present these metaphors as a way of summarizing the current state of resilience interventions and their underlying logic. We then come back to these metaphors throughout the paper as comparison points for presenting our alternative adaptation-based approach to resilience.

One metaphor is “reserve capacity.” Children and youth from socioeconomically disadvantaged backgrounds are presumed to “maintain a smaller bank of resources—tangible, interpersonal, and intrapersonal—to deal with stressful events” (Gallo & Matthews, 2003, p. 34), as they experience more demands on their “resource bank” (e.g., exposures to violence) and thus are able to keep less in reserve. Many resilience interventions seek to address this depletion of physiological and psychosocial resources, such as by providing free or reduced-cost meals to children at school, or by providing school-based health-care, or by fostering positive, supportive relationships with parents, teachers, and/or other competent adults, or by providing safe places for children such as Boys & Girls Clubs (Masten, 2014).

Another metaphor for resilience interventions is “repair and reverse.” Consistent with evolutionary models, this approach recognizes that early adversity alters neural structures in ways that guide socio-emotional development toward faster and more reactive responses to threat, less delay of gratification, and other stress-adapted traits (Blair & Raver, 2012a, 2012b). Because these traits are presumably canalized by early developmental experiences, they can potentially be “repaired and reversed” by altering the contexts of early development (Blair & Raver, 2012a). Toward this end, many resilience interventions seek to change the social contexts of disadvantaged children and adolescents in ways that, through changes in their experiences, recalibrate development toward more “volitional control of attention and emotional arousal for the purposes of reflective, goal-directed action” (Blair & Raver, 2012b, p. 647). Repair and reverse interventions target multiple ecological contexts, but most commonly focus on changing parental behavior to increase responsiveness, consistency, and warmth experienced by the child (e.g., Dishion et al., 2008; Forgatch & Patterson, 2010; Shonkoff & Fisher, 2013). The assumption is that fostering more stable and supportive childhood environments will lead to better social and emotional regulation.

Still another metaphor for resilience interventions is that of a “cat’s claws.” When children from high-risk backgrounds come into the school environment, they tend to arrive like a cat with its claws extended (e.g., insecure attachment, exploitive interpersonal style, hostile attribution bias). While “reverse and repair” interventions target these traits indirectly by altering developmental contexts, other resilience interventions directly target the child. The goal is to get the cat to retract its claws through such methods as promoting more trusting student-teacher relationships, or through social skills training designed to reduce negatively biased social perceptions, improve anger management and emotion regulation, and increase cooperation with peers (e.g., Bullis, Walker, & Sprague, 2001; Durlak, Weissberg, Dymnicki, Taylor, & Schellinger, 2011; Greenberg et al., 2003). The underlying assumption is that, by getting the cat to retract its claws, children will be able to feel more comfortable, connected, and engaged in school and exhibit fewer problem behaviors.

Finally, other resilience interventions can be captured by the "cognitive toolbox" metaphor. Children from high-risk backgrounds may lack certain cognitive tools that are important for school success. Resilience interventions often attempt to build these tools, such as through cognitive-skills training designed to increase executive functions, improve literacy and numeracy skills, enhance critical thinking, and build problem-solving skills. Providing young children with access to preschool-based programs such as Head Start is a common starting point for such interventions. Building a better cognitive toolbox is a central mission of schools and includes such strategies as tutoring, mentoring programs, teacher training, curriculum changes, and after-school programs (e.g., Lauer et al., 2006).

Fighting an Uphill Battle that is Difficult to Win

Whether the goal is to increase reserve capacity, repair and reverse stress-adapted systems, get the cat to retract its claws, or build a better cognitive toolbox, extant intervention strategies share the common goal of trying to get children and youth from high-risk backgrounds to act, think, and feel more like children and youth from low-risk backgrounds. Such interventions involve helping stress-adapted children and youth to compensate for their weaknesses or otherwise overcome the negative effects of growing up under harsh, unpredictable conditions. Although each of the kinds of interventions described by the different resilience metaphors has achieved some empirical success (e.g., Ager, 2013; Durlak et al., 2011; Masten & Cicchetti, 2016), these approaches are ultimately limited because they do *not* attempt to leverage—and thus cannot capitalize on—the unique strengths and abilities that develop in response to harsh, unpredictable environments. Broadly speaking, intervention efforts may be stuck in a pattern of fighting against (rather than working with) functional adaptations to stress (Ellis et al., 2012; Ellis & Del Giudice, 2014).

As a case in point, consider a well-established (and much heralded) finding from the social development literature: The social and cognitive skills that children exhibit in kindergarten, such as prosocial skills and self-control, predict their health, education, and employment outcomes in young adulthood (Duckworth et al., 2012; Jones et al., 2015; Moffitt et al., 2011). While impressive, these results do not mean that children displaying low levels of these skills are impaired (as per the deficit model) or that we should necessarily intervene to improve these skills (as per standard resilience models) (Frankenhuis, Panchanathan, & Nettle, 2016). Two caveats apply that inform the current adaptation-based approach to resilience.

First, among low-SES children and youth, cognitive skills such as self-control may act as a "double-edged sword," facilitating academic success and psychosocial adjustment, while undermining cardiometabolic health (as reflected in obesity, blood pressure, and stress hormones) and inducing faster epigenetic aging (Brody et al., 2013; Chen et al., 2014; Miller et al., 2015). These results challenge the notion of universally "good" or "bad" skills and instead suggest that different skills are likely to be adaptive in different contexts (see especially the discussion below of "successful intelligence" in the Discussion section). For example, although high levels of cognitive control aid performance on goal-based tasks that rely on a narrow focus of attention, low levels of cognitive control (more typical of stress-adapted children and youth) may enhance performance on open-ended tasks that depend on acquiring and using environmental information from diverse sources (Amer, Campbell, & Hasher, 2016).

Second, although children who are fortunate enough to have strong social and cognitive skills in kindergarten have many positive outcomes, many programs that attempt to build such skills in stress-adapted children have had limited success. For example, through an intensive program that targeted stress-adapted children over their first 10 years in grade school, the Fast Track intervention set out to build self-control skills, anger coping strategies, and interpersonal problem-solving skills (Conduct Problems Prevention Research Group, 1992). Although the program cost about $60,000 per child, it had little impact on social-cognitive processes (see Table 1 of Dodge et al., 2013) and, if anything, revealed how difficult it is to get stress-adapted children to think and act more like children from more low-risk backgrounds.

The assumption underlying Fast Track, and other interventions like it, is that children growing up under conditions of poverty and violence are damaged by their experiences, and that we (scientists, policy-makers, educators) can repair that damage through interventions that train stress-adapted children to be more like children from safe, stable environments. Although exposures to high-stress environments certainly jeopardize health and survival (e.g., Mulvihill, 2005; Shonkoff et al., 2009), and traditional interventions approaches are part of the solution to that problem, the challenge is that extant interventions work against, rather than with, social and cognitive adaptations to high-stress environments (Ellis et al., 2012, Ellis & Del Giudice, 2014); thus, *they are fighting an uphill battle that is difficult to win*. Further, interventions have potential costs (including iatrogenic effects) as well as benefits, which vary across developmental contexts. As stated by Ellis et al. (2012):

> From a conditional adaptation perspective, the first question to ask is whether intervention is appropriate. Seemingly harmful risk-taking behaviors may be adaptive in the context of competitive or dangerous environments; therefore, preventing or changing

> these behaviors could be equivalent to declawing the cat—removing the psychological and behavioral weaponry necessary to survive and control resources in one's local ecology (p. 610).

This logic may shed light on the bivalent effects of self-control discussed above. Although self-control may be adaptive for children living in safe, stable environments, high levels of self-control may create a mismatch for children living in harsh, unpredictable environments where opportunities are fleeting and it is important to obtain more immediate rewards (see Mittal et al., 2015; Frankenhuis et al., 2016).

At an applied level, a bigger problem with the deficit approach—including its value judgments regarding putatively desirable versus undesirable capacities and behaviors—is that it is belittling and disrespectful to the members of marginalized and low-income communities who we are trying to engage through policy and interventions. As one community stakeholder noted, "there is a tendency to look at people from underserved communities as somehow inferior" (Acosta et al., 2015, p. 40). In contrast, the adaptation-based approach to resilience recognizes, utilizes, and values the skills and abilities that develop in response to high-risk environments. It emphasizes being appreciated and respected for the skills you do have—and using these skills as building blocks for success—rather than being unappreciated and disrespected for what you lack relative to others.

The Adaptation-Based Approach to Resilience

In contrast to traditional strength-based approaches to resilience, the current adaptation-based approach focuses on generating—and putting to use—a high-resolution map of specific cognitive abilities that are enhanced in children and youth growing up under harsh, unpredictable conditions. The scientific goal is to chart the enhanced social-cognitive skills of individuals who grow up in high-stress environments (see literature reviews below, next two sections), and the applied goal is to leverage these abilities to enhance intervention outcomes in stress-adapted individuals (as discussed in detail below, see Discussion section). Rather than declawing the cat, for example, the adaptation-based approach to resilience considers ways to take advantage of the cat's claws to navigate life's challenges. This adaptation-based approach complements, rather than competes with, traditional strength-based approaches to resilience.

Central to the adaptation-based approach is the concept of trade-offs in development. 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 (e.g., the time spent by an organism looking for food cannot be used to care for offspring). Such constraints dictate that different life domains—bodily maintenance, physical growth, brain development, reproduction—cannot all be maximized at once. Instead, organisms are selected to make tradeoffs that prioritize resource expenditures, so that greater investment of time or resources in one domain occurs at the expense of investment in competing domains. For example, resources spent on an inflammatory host response to fight infection cannot be spent on reproductive effort; thus, the benefits of an inflammatory host response are may trade off against the costs of lower ovarian function in women and reduced musculoskeletal function in men (Clancy et al., 2013; Muehlenbein & Bribiescas, 2010).

According to life history theory (Charnov, 1993; Roff, 1992; Stearns, 1992), these kinds of tradeoffs over development are not random; they have been shaped by natural selection to maximize fitness—survival and reproduction—within the specific environment that an organism develops and in relation to its somatic condition. That means, for example, that organisms growing up in food-rich versus food-poor environments, or in safe versus dangerous environments, or in good versus bad health, face systematically different resource-allocation tradeoffs and constraints. According to life history theory, each trade-off constitutes a decision node in allocation of resources, and each decision node influences the next (opening up some options, foreclosing others) in an unending chain over the life course (Ellis et al., 2009). These tradeoffs progressively favor one developmental trajectory over another, resulting in coherent, integrated suites of physiological and behavioral traits that form the individual's *life history strategy*.

Human life history strategies appear to vary along a dimension of *fast* versus *slow*, reflecting the different tradeoffs that individuals face in different environmental contexts (Del Giudice et al., 2015; Ellis et al., 2009; Figueredo et al., 2006, 2013). Although there is ongoing debate concerning the best way to characterize human life history variation (e.g., Copping, Campbell, & Muncer, 2014; Figueredo et al., 2015), a large body of research suggests that fast life histories are more risky and present oriented (e.g., taking benefits opportunistically with little regard for long-term consequences), prioritize mating effort (e.g., competitive risk-taking, aggression), include earlier sexual development and reproduction, and involve lower levels of parental investment per offspring. By contrast, slower life histories are less risky and more long-term oriented (e.g., greater self-regulation, more investment in long-term relationships, a reciprocally-rewarding interpersonal orientation), include later sexual development and reproduction, and involve higher levels of parental investment per offspring (e.g., Belsky et al., 1991; Chisholm, 1999; Del Giudice et al., 2015; Ellis et al., 2009; Figueredo et al., 2006, 2013; Gibbons et al., 2012).

Variation in the development of life history strategies is sensitive to environmental factors, such as energy availability, extrinsic morbidity–mortality, and predictability of environmental conditions (Ellis et al., 2009; Kuzawa & Bragg, 2012).[3] For example, faster life histories result (in part) from tradeoffs imposed by high levels of extrinsic morbidity–mortality (i.e., external sources of disability and death that are largely insensitive to the adaptive decisions of the organism). In a world of fleeting opportunities and threats without warning, the benefits of investing in morbidity and mortality reduction are low relative to the costs; consequently, future reproduction and other long-term investments are devalued. A fast strategy in this context that maximizes short-term gains (such as through high-risk behaviors that leverage positions in status hierarchies and access to mates) can be expected to enhance fitness despite the long-term costs (Ellis et al., 2012; Frankenhuis et al., 2016; Yao et al., 2014). In total, for both fast and slow strategies, tradeoffs over development function to match the individual to local environmental conditions[4]; depending on those conditions, individuals can benefit from pursuing either faster or slower strategies.

We hypothesize that different skill sets will be associated with fast versus slow strategies, reflecting different cost-benefit trade-offs. As per the specialization and sensitization hypotheses, fast strategists should possess an adaptive suite of social/cognitive skills and abilities that are specialized for thriving in harsh, unpredictable environments (see Ellis & Del Giudice, 2014;

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[3] There is also heritable variation in the development of life history strategies, and observed correlations between environmental exposures and life history strategies may reflect (at least in part) gene-environment correlations (e.g., Barbaro, Boutwell, Barnes, & Shackelford, 2016).

[4] We use the language of "matching" to describe a process through which developmental exposure to a given environmental condition or class of conditions earlier in life (e.g., exposure to violence, harsh childrearing practices, premature disability and death of peers) alters developmental trajectories in ways that, during a species' evolutionary history, enhanced survival or reproduction later in life under comparable conditions, as in the example given here of environmentally-sensitive shifts in the development of life history strategies. Matching is a necessary precondition for the evolution of specialization and sensitization effects. The degree of similarity between early environments and later environments that is necessary for matching to occur (i.e., for developed skills to remain adaptive) is an empirical question—both in terms of levels and types of environmental exposures. Matching depends on the stability of the environment over developmental time (e.g., Rickard, Frankenhuis, & Nettle, 2014; Nettle, Frankenhuis, & Rickard, 2013; Sheriff & Love, 2013).

Frankenhuis & de Weerth, 2013; Mittal et al., 2015), even though those very same skills and abilities may be costly (or less beneficial) in safe, stable environments. For example, an individual growing up in a chaotic/unpredictable environment may prioritize development of attention-shifting skills (to take advantage of fleeting opportunities and avoid unpredictable threats) at the cost of deprioritizing inhibitory control, whereas an individual growing up in a safe environment may make the opposite tradeoffs (see Blackwell et al., 2014, for empirical evidence of such tradeoffs in children).

Although suites of skills should be associated with different life history strategies, we do not expect that all individuals pursuing a particular strategy will have the same skill sets. People should invest in skills and abilities that are relevant in their developmental context. For example, a psychosocially neglected child and a physically abused child can be expected to develop overlapping skill sets that reflect the development of faster life history strategies in both family contexts (e.g., skill sets related to successfully attaining immediate rewards), but non-overlapping skill sets that reflect differential exposures to violence. Thus, there should be divergence in skills and abilities across individuals who differ in levels and types of stress exposures.

In summary, we hypothesize that stress-adapted skills and abilities result from resource-allocation tradeoffs that prioritize expenditures in ways that “make the best of a bad job” (by specializing skills and abilities to match high-adversity contexts), even though “the best” may constitute a high-risk strategy with substantial costs (see above, The Effects of Adversity on Cognitive and Academic Outcomes). These costs reflect the very nature of developmental tradeoffs under harsh conditions (when “reserve capacity” is low): One system is diminished so that another system can be enhanced or preserved (e.g., Muehlenbein & Bribiescas, 2010; Pike, 2005). In the scientific literature on stress, however, these countervailing costs and benefits have not been equally studied. We know vastly more about the detrimental effects of childhood stress than its benefits in context.

The current adaptation-based approach to resilience attempts to address this lacuna. Its larger goal is to uncover the psychological *adaptations* that allow one to successfully navigate the challenges faced in high-stress developmental contexts. This approach converges on a central question: "What are the attention, learning, memory, problem-solving, and decision-making strategies that are promoted by exposures to childhood adversity?" At an applied level, this approach emphasizes: "What do youth from high-risk environments do well?" and "How can we work with, rather than against, these strengths to promote better intervention outcomes?" We now turn to a selective review of empirical studies of the specialization and sensitization hypotheses, focusing on both human and non-human animal literatures.

Literature Review on the Specialization and Sensitization Hypotheses: Animal Research

Consistent with the specialization and sensitization hypotheses, a large body of animal research suggests that early-life stress can enhance cognition and behavior. The majority of these studies have employed either avian or rodent models. Avian species provide a powerful model because of their widely varying life history strategies and because the same species often inhabits many different environments. Rodents provide a strong model for experimental studies of the effects of stress on the brain, behavior, and cognition because of the degree of control that researchers can exert while studying them in the laboratory, and because physiological stress response systems have been highly conserved in the evolutionary history of mammalian species.

Birds

Experimental studies have examined the effects of different forms of early life stress on growth, brain development, cognition, and behavior in birds. The manipulated stressors typically involve either elevated exposure to glucocorticoid hormones (corticosterone is the dominant glucocorticoid in birds) or food restriction (Crino & Breuner, 2015). Although much of this literature has shown that developmental exposures to stress have various negative effects such as decreased immune function, reduced growth, lower neural function, and suppression of sexually selected traits in adulthood (e.g., Hodgson et al., 2007; Pravaosudov et al., 2005; Rubolini et al., 2005; Saino et al., 2005; Spencer et al., 2003), that is only half of the story. The other half is that many avian species respond to stress by calibrating developmental trajectories and skill sets to match high-adversity contexts. This research, summarized in Table 1, has documented a variety of adaptations to early-life stress, ranging from morphological adaptations (e.g., body size, wing morphology, flight speed) to cognitive adaptations (e.g., enhanced food caching memory, enhanced spatial associative learning, innovative foraging tactics) to social adaptations (e.g., novel social learning strategies, attainment of more central social network positions).

Most of the findings reported in Table 1 can be interpreted in the context of the specialization hypothesis (Frankenhuis & de Weerth, 2013): skills and abilities become specialized (and potentially enhanced) for solving problems encountered in harsh, unpredictable environments (e.g., high predation, unpredictable food supply, manipulated corticosterone levels as an internal stress mediator). This specialization has both benefits and costs, as developmental exposures to stress clearly result in a combination of adaptive and harmful effects (reviewed in Crino & Breuner, 2015). As per life history theory, growing up under harsh, unpredictable conditions creates apparent resource-allocation tradeoffs that cause some neural structures to be diminished (i.e., reduced capacity) so others can be enhanced or preserved, thus favoring some abilities over others. Although Table 1 focuses on documented enhancements, avian research on the beneficial phenotypic effects of developmental stress is still in its early stages and dealing with some inconsistent or ambiguous findings. For example, early-life nutritional stress causes deficits in hippocampus-dependent spatial memory but does not impair and may even enhance spatial associative learning (Kriengwatana et al., 2015; Pravosudov et al., 2005; see Schwabe et al., 2012, for analogous findings in humans). *Why* associative stimulus-response strategies may be favored over contextual strategies in the context of early-life nutritional stress remains an open question.

Despite such ongoing questions, researchers have taken steps towards explaining the positive phenotypic effects, documented in Table 1, as adaptations in context. These proposed functional explanations, which mostly constitute hypotheses in need of systematic testing, are reported in the far right column. Overall, the avian literature provides many compelling examples of adaptation in context. In various bird species, growing up under conditions of limited and unpredictable food supplies promotes enhanced food caching ability and memory for stored food locations (Hurly, 1992; Pravosudov & Clayton, 2001, 2002; Pravosudov & Grubb, 1997). Likewise, European starlings exposed to embryonic yolk corticosterone (a reliable indicator of developing into a predator-dense postnatal environment) achieve faster take-off speeds and better in-flight performance, which enhance predator avoidance (Chin et al., 2009; Crino & Breuner, 2015). Finally, zebra finches exposed to corticosterone after hatching more frequently switch between social learning strategies (i.e., discounting of parental information in favor of learning from flock mates), potentially to gain the most updated information about survival-relevant parameters of their habitat (Farine, Spencer, & Boogert, 2015). As summarized in Table 1, the avian literature provides Proof of Principle that developmental exposures to early-life stress can have beneficial phenotypic effects (which presumably enhance fitness).

Rodents

Much of what is known about the effects of early life stress on development comes from a vast rodent literature reported in over 6,000 peer-reviewed research papers extending over a century (reviewed in Howell, Neigh, & Sanchez, 2016). The large majority of this work has been conducted with rats and mice and has extensively examined the effects of both prenatal and postnatal stress (Howell et al., 2016). Much of the post-natal work focuses on observing or manipulating the powerful dam-pup relationship (e.g., maternal separation). Other common developmental stress manipulations include social isolation, restraint stress, social instability stress, social defeat stress, predatory stress, and the combination of multiple stressors. As in the bird literature, much of the rodent literature has shown that developmental exposures to stress have various negative effects such as disrupted HPA-axis and amygdala function, sustained anxiety-like and depressive-like behaviors, lower levels of adult hippocampal neurogenesis, impaired spatial learning and memory, impaired reversal learning, and increased vulnerability to drug abuse and addiction (e.g., Howell et al., 2016; Oitzl et al., 2000; Oomen et al., 2010). This body of work is important and has had many translational implications for understanding the developmental processes and biological mechanisms through which early stress "gets under the skin" to alter the phenotype.

However, these well-documented deleterious effects of stress are not the whole story. The other part of the story is that rodents show coherent developmental responses to ecologically relevant stressors by altering their phenotypes to match high-adversity contexts. This research, summarized in Table 2, has documented a variety of adaptive responses to early-life stress, ranging from reproductive adaptations (e.g., early puberty, greater skill at attracting mates) to cognitive adaptations (e.g., faster fear conditioning, enhanced striatal-dependent response learning, enhanced memory retention for early life events) to social adaptations (e.g., earlier and more frequent play behavior, increased dominance-related behavior and higher social rank).

Although Table 2 reviews documented adaptive phenotypic responses to developmental stress, our ability to draw strong conclusions from the rodent literature has been limited by highly variable findings across laboratories (Macrì, 2013). The first column in Table 2, denoting whether a study tested for specialization or sensitization, may be relevant to explaining this replication problem. If advantages in social and cognitive skills in individuals who grew up under stressful conditions manifest primarily under currently stressful conditions (i.e., sensitization), then simply exposing an animal to developmental stress and then later testing it under generic conditions may not produce interpretable or consistent results. For example, under low-stress conditions in which rats are extensively habituated to testing conditions, rats that received high levels of parental investment from their mothers (i.e., high levels of licking and grooming) show enhanced performance on tests of spatial learning and memory, especially object recognition tests and the Morris water maze (reviewed in Bagot et al., 2009). However, when these highly nurtured rats are tested under high-stress conditions, they show reduced hippocampal long-term potentiation (LTP; a cellular model of learning and memory) and reduced memory on a hippocampal-dependent contextual fear-conditioning task. Consistent with the sensitization hypothesis, it is instead rats that experienced low levels of licking and grooming that excel in these stressful contexts (Bagot et al., 2009; Champagne et al., 2008).

Such sensitization effects may explain why rats who grow up under safe, stable laboratory conditions but then face acute stressors in adulthood (e.g., predation stress, restraint and tail shock, food restriction) show widely variable outcomes: they are not developmentally prepared to cope with these challenges (Macrì, 2013). A core assumption of the current adaptation-based approach to resilience is that individuals growing up in harsh, unpredictable environments specialize their cognitive abilities to match high-adversity contexts, as did the rats that experienced low levels of licking and grooming and then coped more successfully with acute challenges in adulthood. In the rodent literature, many of the studies documenting beneficial phenotypic effects of developmental stress exposures have employed this kind of a sensitization design (Table 2), in which the adult stress task is reminiscent of earlier life conditions.

Despite some ongoing issues regarding contradictory findings in the rodent literature, researchers have made steps toward explaining the beneficial phenotypic effects documented in Table 2 as adaptations in context. As in the avian literature, the rodent literature provides many apparent examples of functional adaptations to stress. As shown in Table 2, several of these cases involve specialization. For example, rodents exposed to various early-life stressors tend to prioritize development of the striatal-dependent *associative learning and memory system* (also commonly referred to as a "stimulus-response" system), which supports immediate responding to environmental challenges (Kim et al., 2001; Lemaire et al., 2000; Leong & Packard, 2014; Park et al., 2008). Likewise, maternal deprivation early in life promotes developmental tradeoffs favoring current over future reproduction (i.e., rodents shift toward faster life histories), including accelerated pace of development, more socially competitive behavior, greater skill at attracting mates and achieving social dominance, and more competitive success at getting pregnant (Cameron et al., 2008; Franks et al., 2015; Parent et al., 2012; Parent & Meaney, 2008; Sakhai et al., 2011).

In other cases, as summarized in Table 2, adaptation in context involves sensitization. For example, rats that were exposed to a regimen of stressors in adolescence (i.e., encounters with predators, unpredictable social and physical stressors), compared with rats in an unstressed control condition, showed enhanced performance on a timed foraging task (i.e., they were more efficient at transitioning between foraging patches and consumed more food) when tested under high-threat conditions (i.e., predation cues, bright lights) (Chaby, Sheriff, Hirrlinger, & Braithwaite, 2015a). Likewise, developmental matching between the early programming environment (maternal deprivation) and the later adult environment (e.g., alarm bells, food deprivation, restraint) resulted in better hippocampal-dependent performance in a contextual fear conditioning test and enhanced contextual memory (Zalosnik et al., 2014).

Taken together, a growing body of comparative avian and rodent research supports both the specialization and sensitization hypotheses: harsh and unpredictable early-life environments do not solely impair behavior and cognition but specialize it for solving recurring adaptive problems faced in high-adversity contexts. The human literature, to which we now turn, also provides reasonable support for these hypotheses.

Literature Review on the Specialization and Sensitization Hypotheses: Human Research

As discussed earlier, the deficit model is the prevailing approach to studying the effects of stress on human development. This approach has been productive in mapping the pathways and mechanisms through which early-life stress disrupts neurobiological systems and cognitive development (see above, The Effects of Adversity on Cognitive and Academic Outcomes). The success of this approach, however, and the resulting dominant position of the deficit model in the field, has largely foreclosed consideration of the functional role of adaptations to stress in regulating normal variation in development across diverse contexts. Consequently, we know relatively little about beneficial phenotypic effects of developmental exposures to stress. However, with the recent emergence of evolutionary-developmental models, and especially life history theory, in the psychological sciences (e.g., Belsky et al., 1991; Del Giudice et al., 2011; Ellis & Del Giudice, 2014; Frankenhuis & de Weerth, 2013; Frankenhuis et al., 2016; Griskevicius et al., 2011; Wenner et al., 2013), such beneficial effects have started to receive increasing attention.

There are two basic challenges in studying the effects of stress in regulating human development. First, the human literature is inherently limited relative to the avian and rodent literatures because early-life stress can only be measured and not experimentally manipulated. Thus, our state of knowledge is largely correlational. Second, although current stress exposures can be experimentally manipulated (e.g., through priming), ethical constraints dictate that those manipulations are relatively mild; many ecologically valid forms of threat and danger cannot be studied experimentally. Despite these limitations, there is wide variation in childhood exposures to harshness and unpredictability, and that variation can be validly measured (e.g., Belsky et al., 2012; Raver et al., 2015; Simpson et al., 2012). Further, a large corpus of research has shown that even the limited stress manipulations employed by psychologists can have substantial effects on human cognition and behavior (e.g., Griskevicius et al., 2011; Hill et al., 2013; Mittal et al., 2015). Taken together, these factors enable meaningful (though less than definitive) tests of the specialization and sensitization hypotheses in humans.

An emerging body of human research has begun to document how early stress exposures regulate the development of skills and abilities to match high-adversity contexts. This research, summarized in Table 3, has documented a variety of adaptations to early-life stress, ranging from enhanced social-emotional skills (e.g., emotion recognition, empathic accuracy) to enhanced memory in specific domains (e.g., early-life memory retention; memory for negative, emotionally-laden, or stressful events; working memory in the form of rapid tracking and memory updating) to enhanced learning in specific domains (e.g., learning about animal danger, procedural learning) to enhanced cognitive speed and accuracy in specific domains (e.g., recognition of angry or fearful faces) to enhanced attention-shifting ability.

The findings summarized in Table 3 primarily focus on one part of the story: beneficial phenotypic effects. The other part of the story—detrimental phenotypic effects—has already been extraordinarily well documented (as reviewed above, The Effects of Adversity on Cognitive and Academic Outcomes). A well-rounded analysis thus suggests that developmental exposures to stress have a mix of adaptive and harmful effects, as highlighted by several of the entries in Table 3 (e.g., exposure to interparental verbal aggression improves, but exposure to interparental physical aggression reduces, accuracy at recognizing emotions; Raver et al., 2015). Such mixed findings may reflect, in part, inadequate attention to sensitization effects (in terms of matching between earlier and later stress exposures). For example, human infants show reduced psychomotor and mental development during the first year of life when they have been exposed to discordant, as opposed to concordant, levels of prenatal and postnatal maternal depression, even though the concordant condition involves greater cumulative exposure to stress (Sandman, Davis, & Glynn, 2012). Studies that have examined the effects of maternal depression, anxiety, and stress during pregnancy on child cognitive outcomes, without taking into account matching with postnatal environments, have produced mixed results (e.g., DiPietro et al., 2006; Glover, 2014).

Many of the findings reported in Table 3 can be interpreted as adaptations in context. Several cases involve specialization. For example, children who have experienced severe neglect or abuse tend to exhibit improved detection, learning, and memory on tasks involving stimuli that are ecologically relevant to them (reviewed in Frankenhuis & de Weerth, 2013), such as enhanced memory for a doctor who performed an invasive examination (Eisen et al., 2007), or enhanced recall of distracting aggressive stimuli (e.g., guns, swords) (Rieder & Cicchetti, 1989), or faster orientation to angry faces and voices (Pollak, 2008; Pollak et al., 2009). These cognitive skills may promote survival in hostile environments. Other research conducted with more normative samples also supports the specialization hypothesis. Much of this work employs SES as an indicator of developmental stress. One significant finding to emerge from this literature is that lower-SES individuals have an advantage in social-cognitive tasks involving contextual information, such as the ability to accurately read others' affective states (reviewed in Kraus et al., 2012). For example, in one study, high school-educated university employees outperformed college-educated university employees on a standard test of empathic accuracy (which involved labeling, with emotion terms, different posed facial expressions) (Mayer, Salovey, & Caruso, 2002). Enhanced empathic accuracy may promote behavioral prediction and management of external social forces and individuals that exert substantial control over one's life (which occurs chronically for people at low SES) (see Kraus et al., 2012).

In other cases, as summarized in Table 3, adaptation in context involves sensitization (whereby skills and abilities promoted by exposures to early-life stress are enhanced under currently stressful conditions that are reminiscent of earlier childhood experiences). For example, individuals who grew up under conditions of low socioeconomic status (SES; compared with others who grew up under high SES conditions) show enhanced procedural learning (i.e., stimulus–response mapping in categorization tasks), but reduced performance on cognitive functions that rely heavily on working memory, when tested under primed conditions of high financial demand (Dang et al., 2016; Mani et al., 2013). Although procedural learning may be enhanced under the kinds of high-stress conditions that chronically occur at low SES, procedural learning processes apparently trade off against working memory (DeCaro et al., 2008).[5] Likewise, in a longitudinal study of a children born into poverty, adults who experienced high family unpredictability during their first 10 years of life (i.e., parental transitions, residential changes, parental job changes), compared with others who experienced low family unpredictability, showed enhanced ability in attention shifting (a component of executive function that involves efficiently switching between different tasks) when tested under conditions of primed economic decline/uncertainty (Mittal et al., 2015). Unpredictable early-life environments also enhance aspects of working memory central to tracking novel information in the environment. Youth who grew up under more unpredictable environmental conditions, compared with others who were reared in more predictable environments, were able to track a larger amount of information in their working memory when tested under conditions of primed economic decline/uncertainty (Young, Griskevicius, Simpson, Waters, & Mittal, 2016). These kinds of enhanced abilities in attention shifting and working memory are likely to promote the detection of threats and taking advantage of fleeting opportunities in chaotic/unpredictable environments. At the same time, these enhanced skills may trade off against poorer inhibitory control (Mittal et al., 2015) and worse performance on aspects of working memory that involved long-term storage and information retention in the face of distraction (Young et al., 2016).

In total, research in birds, rodents, and humans suggests that developmental exposures to stress can improve forms of attention, perception, learning, memory, and problem solving that

[5] We are assuming tradeoffs here due to inverse correlations in performance. However, this inverse correlation could be mediated by a third variable (and thus not present in all contexts).

are ecologically relevant in harsh or unpredictable environments. These findings suggest that early-life stress not only impairs cognitive development (as in the well-documented negative phenotypic effects) but also directs or regulates cognitive development toward prioritizing skills and abilities that are adaptive in context (as per the specialization hypothesis). Many of these skills and abilities, moreover, are primarily manifest in currently stressful contexts where they would provide their most powerful fitness-relevant advantages (as per the sensitization hypothesis).

Discussion

How does repeated or chronic childhood adversity shape biobehavioral development and, through it, social and cognitive abilities? In the developmental sciences, there is a widely accepted answer to this question. Instantiated in various deficit models, such as *cumulative risk* (e.g., Evans et al., 2013; Sameroff et al., 1987; Seifer et al., 1996), *toxic stress* (Shonkoff et al., 2012), and *allostatic load* (Lupien et al., 2006; McEwen & Stellar, 1993), that answer posits a striking duality: biobehavioral responses to stress may be adaptive in the short term, but protracted activation of stress responsive systems is maladaptive and toxic in the long term. Repeated or chronic childhood adversity causes disruptions of brain structure and function, resulting in dysregulation of neurobiological mediators "that are the precursors of later impairments in learning and behavior as well as the roots of chronic, stress-related physical and mental illness" (Shonkoff et al., 2012, p. e236). In these deficit models, children from high-stress backgrounds are considered to be at risk for impaired development, and the intervention goal is to prevent, reduce, or repair the damage.

Steps toward achieving that goal began with correlational studies to identify the attributes and contexts of children who "beat the odds" despite high exposures to adversity, followed by the development of interventions to promote those attributes and contexts. These resilience interventions share the common goal of getting children and youth from high-risk backgrounds to act, think, and feel more like children and youth from low-risk backgrounds. As discussed above (The Traditional Strength-Based Approach to Resilience), these interventions can be captured by such metaphors as "increasing reserve capacity," "repairing and reversing" stress-adapted systems, "getting the cat to retract its claws," and "building a better cognitive toolbox."

Missing from traditional intervention strategies is an attempt to leverage the unique strengths and abilities that develop in response to high-stress environments. As instantiated in the specialization and sensitization hypotheses, a core assumption of evolutionary-developmental models is that exposures to stress do not so much impair development as direct or regulate it toward strategies that are adaptive under stressful conditions (see above, The Adaptation-Based Approach to Resilience). From this perspective, deficit models miss something fundamental about development: They miss the coherent, functional biobehavioral changes that occur in response to stress over time, including regulation of alternative life history strategies (Ellis & Del Giudice, 2014). These changes not only promote adaptation to harsh, unpredictable childhood environments (as reflected in such traits as heightened vigilance, attention shifting, and empathic accuracy), but also shape longer-term developmental trajectories to match expected future conditions. Fast life histories involve prioritizing investment in specific skills and abilities that enable one to survive and reproduce under harsh, unpredictable conditions, even though those very same skills and abilities may be costly (or less beneficial) in safe, stable environments.

The implications of this theory are far-reaching. If individual differences in skills and abilities largely reflect adaptation in context, then stress-adapted individuals growing up in harsh, unpredictable environments should develop heightened skills and abilities relevant to solving adaptive problems faced in those environments (specialization) and might outperform individuals growing up in safe, stable environments when tested under conditions resembling the high-risk contexts to which they are ostensibly adapted (sensitization). As reviewed in Tables 1-3 and discussed in the previous two sections, research in birds, rodents, and humans suggests that developmental exposures to stress can improve forms of attention, perception, learning, memory, and problem solving that are ecologically relevant to survival and reproduction in harsh, unpredictable environments. Although the effects of early life stress are clearly mixed with a combination of positive and negative effects, the current literature suggests that exposures to adversity regulate cognitive development toward prioritizing skills and abilities that are adaptive in context (as per the specialization hypothesis). Many of these skills and abilities, moreover, are primarily manifest in currently stressful contexts where they would provide the greatest fitness-relevant advantages (as per the sensitization hypothesis).

Successful Intelligence

Our adaptation-based approach to resilience converges with Sternberg's (1999, 2014a) theory of *successful intelligence*:

> Successful intelligence is one's ability to choose and successfully work toward the attainment of one's goals in life, within one's cultural context or contexts. … *What differs is the nature of the problems encountered in various ecological contexts* (Bronfenbrenner, 1979). For example, one child may focus during the day on how to solve an algebra problem, another on how to get past drug dealers on the way to school, another on how to ice-fish so that his family has something to eat for dinner. The mental processes may be similar or identical—what differs is the kinds of knowledge and skills to which they give rise … (Sternberg, 2014, p. 209, emphasis added).

Evidence for the theory of successful intelligence comes from studies in diverse populations (Sternberg et al., 2000). For instance, rural Kenyan children who do poorly in school know the names of natural anti-parasitic medicines that could save their lives (Sternberg et al., 2001). Yup'ik Eskimo children who also do poorly in school are able to ice-fish, hunt, and negotiate difficult geographic environments (Grigorenko et al., 2004). Young Brazilian street vendors that are unable to solve arithmetic problems presented to them abstractly in paper-and-pencil format solve comparable problems, quickly and accurately, while selling and buying goods on the market (Schliemann & Carraher, 2002). These findings demonstrate the importance of viewing intelligence as developing expertise (Sternberg, 2014b) and underscore the need to consider social-cultural context in studying skills and abilities (Greenfield, 2014; Rogoff, 2003; Sternberg et al., 2000). Consistent with the theory of successful intelligence, we conceptualize childhood adversity as a social-ecological context that gives rise to particular skills and forms of knowledge (as per the specialization and sensitization hypotheses).

Implications for Education and Intervention

The current focus on adaptation in context supports an alternative view of resilience that centers on leveraging the unique strengths and abilities that develop in response to high-stress environments. The better we understand these strengths and abilities, the more effectively we can tailor education, policy, and interventions to fit the needs and potentials of stress-adapted children and youth. The adaptation-based approach to resilience converges on a central question: "What are the attention, learning, memory, problem-solving, and decision-making strategies that are promoted by exposures to childhood adversity?" At an applied level, this approach emphasizes: "What do children and youth from high-risk environments do well?" and "How can we work with, rather than against, these strengths to promote better intervention outcomes?" Ellis, Volk, Gonzalez, and Embry (2015) provide an example of this approach to intervention.

The adaptation-based approach to resilience conceptualizes stress-adapted children and youth as being cognitively "gifted" for functioning in harsh, unpredictable environments. Instead of recognizing these gifts, however, and using them as building blocks for success, such gifts are rarely measured or properly understood in Western school systems. This is because a "good student" is essentially defined as a slow life history strategist (as epitomized by such traits as self-management, relationship skills, responsible decision making, and setting and achieving positive goals). Such an approach is regrettable because it creates a *mismatch* between the types of social/cognitive skills possessed by fast strategists and the kinds of social/cognitive skills that are needed to function well in school.

Reflecting the dominant position of the deficit model in developmental and clinical science, the current state of the field is an absence of empirical data on what stress-adapted children and youth are good at (for the few exceptions, see Table 3). Because knowledge is so limited in this domain, the field lacks an empirical basis for developing interventions that leverage the unique strengths and abilities that develop in response to high-risk environments. This lacuna provides an opportunity and agenda for the future: If hypotheses regarding enhanced skills and abilities in stress-adapted children and youth garner support, the impact would be transformational. Rather than narrowly focusing on what children and youth from harsh environments cannot do, the floodgates would open for exciting research on what such individuals can do well, with far-reaching implications for interventions that leverage the talents of stress-adapted children and youth as building blocks of success, enabling a wider range of individuals to achieve their full potential.

Consider teaching and learning strategies. There is a set of standard instructional practices for teaching subjects such as reading and math. For children growing up under harsh, unpredictable conditions (who display lower levels of reading, language, and math skills that are already evident in kindergarten; see above, The Effects of Adversity on Cognitive and Academic Outcomes), these standard practices are often supplemented by a variety of targeted interventions designed to improve academic performance. As discussed earlier (The Traditional Strength-Based Approach to Resilience), these intervention strategies can be captured by such metaphors as “declawing the cat” (e.g., building student-teacher trust), “reverse and repair” of stress-adapted systems (e.g., enhancing social and emotional learning), increasing “reserve capacity” (e.g., National School Lunch Program), and building a better “cognitive toolbox” (e.g., small group academic tutoring, Head Start). These supplemental strategies attempt to ameliorate the social and physical challenges faced by at-risk students and/or provide extra academic support.

A key limitation of these approaches is that, although at-risk students receive supplemental services and support, underlying pedagogical strategies do not differ for children and youth growing up under—and potentially adapted to—different socio-ecological conditions. These strategies include such approaches as (a) introduction of alternative textbooks/curricular content to improve student outcomes, (b) use of computer-assisted instruction to assess students’ performance levels and tailor exercises accordingly, and (c) professional development programs to enhance teachers’ instructional practices and classroom management strategies (e.g., Slavin & Lake, 2008). *Each of these three approaches could be revised and extended in light of the current adaptation-based approach to resilience.*

A. Curricular Content. The adaptation-based approach has implications for the types of content that best facilitate learning. Right now, the introduction of alternative textbooks/curricular content focuses on topics such as developing critical concepts and problem solving skills and improved sequencing of objectives. The emphasis is on evidence-based practices that work at the classroom or school level. This approach could potentially be extended to enhance learning in stress-adapted children and youth by incorporating concepts and problem solving skills that are ecologically relevant in harsh, unpredictable environments. For example, because perceptions of social rank are especially relevant to youth from low SES backgrounds (Kraus et al., 2012), they may be particularly motivated and able to solve reasoning problems that are related to social status and dominance. Consider the following logical reasoning problem: Adam is older than Bart, and Bart is older than Chris; who is older, Adam or Chris? An adaptation-based approach suggests that students from high-risk backgrounds may be better at solving this problem when the content concerns status and rank. For example, Adam is dominant over Bart, and Bart over Chris; who is dominant, Adam or Chris? More research is obviously needed, but the idea that stress-adapted youth could learn complex reasoning more easily by having it taught via specific content has powerful implications. Once they have mastered such basic problems, they could more easily learn to generalize them to other contexts, including abstract ones that are important in higher education (Barnett & Ceci, 2002).

The problem with current standardized testing procedures is that they do not employ content or contexts that match the unique skills and abilities of stress-adapted children and youth. The resulting mismatch essentially rigs these tests against people who grow up in harsh, unpredictable environments. That mismatch can be debilitating for performance on standardized tests like the SAT or ACT, which assess skills and abilities that are believed to be important for academic success at the university level. From an adaptation-based perspective, however, that is a narrow definition of success; it neglects the kinds of stress-adapted skills and abilities that are instantiated in fast life history strategies (see especially the preceding discussion of *successful intelligence*). To improve learning, achievement, and career outcomes in stress-adapted children and youth, pedagogical strategies should be adapted to capitalize on these strengths.

B. Information Delivery. The adaptation-based approach to resilience has implications for the delivery of information to facilitate learning among stress-adapted children and youth. Currently, computer-assisted instruction focuses on identifying children's strengths and weaknesses and then customizing self-instructional exercises to fill in gaps in skills and knowledge. This approach could potentially be extended to evaluating stress-adapted skills and abilities, and then tailoring exercises to leverage identified strengths. For example, if students growing up in stressful environments have difficulty sustaining attention but are experts at shifting their attention between different tasks (Mittal et al., 2015), then approaches to instruction that leverage this style could potentially facilitate learning (e.g., stress-adapted students might learn more effectively in environments that use dynamic touch-screens rather than static print). Likewise, if students growing up in stressful conditions are especially good at tracking the amount of information in their environment (Young et al., 2016), this enhanced working memory might lead them to excel when learning in information-rich environments that require quick decisions. Although future research is needed to better understand how stress-adapted students learn most effectively, the explosion of online learning, including at the middle school and high school levels, greatly increases the potential for computer-assisted instruction to be customized for specific students. For example, two students could take the same Algebra course, but the course materials could be presented to each student in different ways— utilizing different skills and abilities that largely reflect adaptations in context—in order to maximize learning.

In this way, instructional methods could move beyond a “one size fits all” approach to work with, instead of against, social and cognitive adaptations to stress. Standard educational practices, which are invariably developed in relation to normative student populations, fail to capitalize on the unique strengths and abilities that develop in response to high-stress environments. Many traditional interventions instead attempt to “reverse and repair” adaptations to stress (as discussed above, see The Traditional Strength-Based Approach to Resilience). This narrow approach undervalues the skills and abilities that stress-adapted individuals bring to society.

C. Instructional Practices. The adaptation-based approach to resilience has implications for enhancing teachers’ instructional practices, including creating school environments that are more conducive to learning in stress-adapted students and testing conditions that enable such students to adequately display their skills and knowledge. Many teachers receive professional development training on the use of instructional process strategies (e.g., to increase student motivation or implement cooperative learning). This approach could potentially be extended to providing professional development on how to work with adaptations to stress to help students achieve their full potential.

As per the sensitization hypothesis, many of the strengths and abilities of children and youth from high-risk backgrounds are context-dependent, such as when people who grow up in unpredictable environments perform better on cognitive tests in contexts that are not stress-free (Mittal et al., 2015; Young et al., 2016). This context-dependency requires rethinking the standard practice of teaching and evaluating children under quiet, controlled environmental conditions. For people who grew up in loud, chaotic environments, it may disadvantage them to have to perform certain tasks under sterile, quiet conditions, which are unfamiliar and might not elicit their optimal cognitive performance. Stress-adapted children and youth may instead perform certain tasks better in settings that do not attempt to minimize movement or suppress the reality of daily uncertainties. This might include environments that expressly highlight the prevalence of daily stressors (e.g., reminders that we live in world where resources are uncertain) or environments in which people in a room are allowed to move and talk, which may simulate the contexts in which they developed their skills. Such an approach fits with work in other populations, such as children with attention-deficit hyperactivity disorder (ADHD). Recent studies of these children have shown that their performance is enhanced (more than that of controls) if they are allowed to learn while moving around (Hartanto et al., 2015; Sarver et al., 2015), potentially because children with ADHD are better able to concentrate under those conditions. Research is critically needed to delineate the contexts that maximize performance of stress-adapted children and youth (see also Richardson, Castellano, Stone, & Sanning, 2016).

Finally, the adaptation-based approach has implications for careers and personnel selection. For example, a human resources manager in the military recently approached one of us. She explained that while many people in the military do well in the classroom, the same people often perform poorly in the field, where they often need to quickly switch from task to task in a stressful environment. This need for task-shifting under stress is reminiscent of the timed-foraging task that Chaby et al. (2015a) created for rats to assess how efficiently they transitioned between multiple foraging patches in an open arena in the presence of visual and auditory cues of avian predation. Rats that had previously experienced chronic stress during adolescence showed superior performance on this task. Knowledge of this kind of sensitization effect could help human resource managers identify individuals who will perform at high levels under stressful, changing conditions. More generally, explication of specialization and sensitization effects should have great relevance for job training and placement among stress-adapted youth.

Conclusion

Comparative research on birds, rodents, and humans highlights the role of stress in regulating development of adaptively-relevant skills and abilities. Leveraging these strengths could help stress-adapted individuals achieve their full potential and lead more satisfying and productive lives. The adaptation-based approach to resilience thus converges on a pressing research agenda: to uncover a high-resolution map of the skills and abilities of children and youth from high-risk backgrounds (specialization), and to determine how developmental exposures to stress interact with current psychological states and conditions to regulate learning and performance (sensitization). In pursuing this agenda, the field will need to pay careful attention to types of developmental stress (e.g., acute vs. chronic vs. unpredictable), the timing of stress exposures (e.g., sensitive periods, delays between developmental stress exposures and the manifestation of beneficial/detrimental effects), and their interaction with current states (under what conditions, and for which cognitive abilities, do we expect to observe sensitization effects?). Addressing such questions will require continued research efforts from behavioral scientists coupled with increased dialogue and collaboration with teachers, workforce development specialists, and other community-engaged professionals who work with stress-adapted children and youth. Such cross-disciplinary interaction should promote a better understanding of how classroom environments, instructional strategies, job training, and related domains can be designed to support stress-adapted individuals in ways that converge with their life experiences to leverage their unique skills and abilities. Interdisciplinary collaboration will be critical for translating basic research into applications that enhance educational and life outcomes in children and youth growing up under harsh, unpredictable conditions. Although much research needs to be done, this work holds the promise for transformative interventions that work with, instead of against, the skills and abilities of individuals from a diverse range of life circumstances.

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Table 1.
Developmental Stress: Evidence for Adaptive Phenotypic Effects in Birds

Hypothesis type	**Developmental Stress Exposure**	**Phenotypic Effects**	**Proposed Function**
Speciali-zation	Embryonic exposure to yolk corticosterone	Production of smaller nestlings that achieve faster take-off speeds (barn swallows, European starlings, great tits: Crino & Breuner, 2015). Enhanced flight as shown by more mature flight muscles, lower wing loading, and better in-flight performance by fledglings (European starlings: Chin et al., 2009).	Enhanced flight capacity promotes survival in predator dense environments (as signaled by maternal and embryonic glucocorticoids).
Speciali-zation	Low food access-ibility, early-life social isolation (in nestlings/ fledglings)	In adulthood, enhanced associative learning (zebra finches: Brust et al., 2014; Kriengwatana et al., 2015; chickens: Goerlich et al., 2012) but impaired hippocampal-dependent contextual learning on spatial tasks (Western scrub-jays: Pravosudov et al., 2005; zebra finches: Kriengwatana et al., 2015).	Enhanced associative learning (over slower, cognitively-expensive contextual learning) promotes *immediate* responding to environmental challenges (prevalent in resource-poor environments).
Speciali-zation	Unpredictable stress regimen (e.g., catching, handling, noise) as fledglings	Within 6 days following stress exposure: Enhanced prefrontal cortex-dependent reversal learning (i.e., flexibility relearning a new rewarded location) in a spatial task (Japanese quail; Calandreau et al., 2011).	Enhanced reversal learning promotes survival in an unpredictable environment.
Speciali-zation[1]	Limited and unpredictable food supply[1]	Enhanced food caching intensity and memory for cache location (i.e. spatial memory; black-capped chickadees, tufted titmice, marsh tits: Hurly, 1992; Pravosudov & Grubb, 1997; Pravosudov & Clayton, 2001, 2002).[2]	Enhanced food caching and memory for stored food locations promotes survival and reproduction in environments where food is scarce or unpredictable.

Speciali-zation	Post-hatching exposure to corticosterone	In adulthood, more frequent switching between social learning strategies (i.e., discounting of parental information in favor of learning from non-parental adults); weaker affiliation with parents in favor of flock mates; attainment of more central social network positions; improved performance on a novel foraging task; higher quality and quantity of offspring in males (zebra finches: Boogert, Farine, & Spencer, 2014; Crino et al., 2014a, 2014b; Farine et al., 2015).	In unpredictable environments, exposure to elevated developmental stress (as signaled by glucocorticoids) may indicate one's parents are struggling to cope with current conditions. If other adults know better, copying them should yield better foraging strategies. Chicks may also be selected to switch to individual trial-and-error learning in this context. Elevated corticosterone triggers life history tradeoffs (e.g., shorter lifespan) favoring current over future reproduction.
Speciali-zation	Pre-hatching exposure to corticosteroids; post-natal food unpredictability (nestlings and fledglings)	In adulthood: Pre-hatching stress led to increased activity level, exploration in a novel environment, and mimicking of foraging strategies demonstrated by conspecifics; post-hatching stress led to more risk-taking to find food and avoidance of foraging strategies demonstrated by conspecifics. Combined pre- and post-hatching stress resulted in the highest levels of exploratory and risk-taking behavior (Japanese quail: Boogert et al., 2013; Zimmer et al., 2013).	Elevated exploratory and risk-taking behavior under developmentally stressful conditions promotes greater food acquisition. Food unpredictability promotes novel foraging strategies relative to those demonstrated by conspecifics.
Sensiti-zation	Low-quality diet as nestlings	During a brief period of food restriction, adult zebra finches that experienced poor early nutrition were faster to engage in exploratory and foraging behavior (Krause et al., 2009).	Rapid exploration and foraging promotes greater food acquisition in a nutritionally poor environment.

[1]Timing of developmental stress exposure not specified. [2]Age at testing not specified.

Table 2.
Developmental Stress: Evidence for Adaptive Phenotypic Effects in Rodents

Hypothesis type	**Developmental Stress Exposure**	**Phenotypic Effects (age at testing)**	**Proposed Function**
Speciali-zation	Prenatal stress (repeated restraint of dams during pregnancy); predator stress, restraint and tail shock (in adults)	Impaired hippocampus-dependent place learning (juveniles and adults; Kim et al., 2001; Lemaire et al., 2000; Park et al., 2008; Wu et al., 2007), but enhanced striatal-dependent response learning and biased use of response learning on tasks that can be solved using either place learning or response learning (i.e., *dual* solution tasks) (adults; Kim et al., 2001; Leong & Packard, 2014).	Enhanced stimulus-response/associative learning (over slower, cognitively-expensive contextual learning) promotes immediate responding to environmental challenges in a dangerous world (as signaled by various developmental stress exposures).
Speciali-zation	Juvenile exposure to elevated platform stress followed by adult exposure to acute swim stress	Rats that experienced both juvenile and adult stress (compared with rats that had experienced juvenile stress only, adult stress only, or no stress) displayed greater anxiety and enhanced spatial learning and memory as evidenced by performance in the Morris water maze (adults; Avital & Richter-Levin, 2005).	Match between juvenile programming environment and later adult environment promotes effective coping with danger (e.g., anxious/defensive behaviors and enhanced spatial learning/memory improve predator-avoidance.)
Speciali-zation	Low maternal licking and grooming (infancy); earlier age at weaning (postnatal day 21-28)	Earlier and more frequent play behavior (pre-weaning period; Franks et al., 2015); females: increased dominance-related behaviors and higher social rank (adults; Parent et al., 2012); males: higher levels of play fighting (juveniles; Parent & Meaney, 2008) and stronger defensive responses to an intruder (adults; Menard & Hakvoort, 2007).	Heightened pace of social development, more socially competitive behavior, and stronger defensive responding promote survival and earlier reproduction in harsh, competitive environments (as signaled by low maternal investment).
Speciali-zation	Low maternal licking and grooming (infancy)	In females, earlier puberty and greater skill at attracting mates; in a competitive mating context, greater success at getting pregnant (adults; Cameron et al., 2008; Sakhai et al., 2011; Parent et al., 2012).	Harsh, unpredictable environments (as signaled by low maternal investment) promote tradeoffs favoring current over future reproduction.

Speciali-zation/ Sensiti-zation	High maternal stress (produced by poor nesting materials during postnatal days 1-6); maternal deprivation (daily separations during first 2 wk of life)	Accelerated maturation of (a) brain regions important for emotion expression, associative learning, and memory and (b) behaviors supported by these regions (e.g., faster fear conditioning, slower fear extinction, enhanced memory retention for early life events) (post-natal days 7-47: infancy to adolescence; Callaghan & Tottenham, 2016a, 2016b; Richardson, Cowan et al., 2016).	Stress acceleration hypothesis: Accelerated maturation reflects the allocation of developmental resources toward emotional systems and associative learning and memory in ways that confer a survival advantage through earlier self-regulation in harsh environments (as signaled by absent or inconsistent parental care) (Callaghan & Tottenham, 2016a).
Speciali-zation/ Sensiti-zation	Predator exposure, social and physical stress (e.g., crowding, damp bedding) in adolescence	Faster decision-making (shorter time to correct a choice and locate a food reward after an error); faster to explore novel environments and objects; enhanced reversal learning; increased monitoring of environment for threats; under currently threatening conditions (predation cues, bright lights), rats that experienced stress during adolescence performed better in a timed-foraging task (adults; Chaby et al., 2013, 2015a, 2015b, 2016).	Faster decision-making and exploratory behavior, heightened vigilance, and reversal learning promote survival in harsh, unpredictable environments. Match between adolescent programming environment and current conditions promotes more successful foraging under threat.
Sensiti-zation	Low maternal licking and grooming (infancy); maternal deprivation (24 hr separation at postpartum day 3)	Under low-stress conditions, reduced performance on tests of spatial learning and memory; but under high-stress conditions, enhanced hippocampal long-term potentiation (a cellular model of learning/memory) and enhanced memory on a hippocampal-dependent contextual fear-conditioning task (adults; Bagot et al., 2009; Champagne et al., 2008; Oomen et al., 2010).	Harsh, unpredictable early programming environments (as signaled by low maternal investment) prepare the animal to function under conditions of adversity later in life.
Sensiti-zation	Maternal deprivation (daily separations over first 3 wk of life); unpredictable stress in early adulthood	Following the unpredictable stress regimen, rats that had experienced maternal deprivation (compared with rats that had not) showed better hippocampal performance in a contextual fear conditioning test and enhanced contextual memory (adults; Zalosnik et al., 2014).	Match between early programming environment and later adult environment promotes survival in dangerous environments through enhanced contextual fear conditioning and memory.

Table 3.
Developmental Stress: Evidence for Adaptive Phenotypic Effects in Humans

Hypothesis type	Developmental Stress Exposure	Phenotypic Effects (age at testing)	Proposed Function
Speciali-zation	Interparental aggression (6, 15, 24, 35, and 58 mos.)	More exposure to interparental verbal aggression predicted greater accuracy at recognizing emotions (joy, sadness, anger, and fear); but more exposure to interparental physical aggression predicted lower emotion recognition accuracy (58 mos.; Raver et al., 2015).	Enhanced emotion recognition improves behavior prediction, which is vital to survival in hostile environments. Negative effect of physical aggression constitutes impairment (e.g., neurobiological disruption).
Speciali-zation	Parental divorce/ separation (< 7 yrs.); exposure to stepparents and other extra adults while growing up	Early exposure to divorce, greater separation stress, and more non-biological-parent adults in the household were associated with earlier memory retention (i.e., recall of earlier childhood events; Artioli et al., 2012, 2015; Artioli & Reese, 2014).[1]	Stress acceleration hypothesis (Callaghan & Tottenham, 2016a; described in Table 2).
Speciali-zation	Low maternal age, maternal smoking during pregnancy, low family SES (early childhood)	Enhanced performance on response shifting but lower performance on verbal memory in kindergarteners (Vandenbroucke et al., 2016).	Enhanced response shifting promotes anticipation of threats and fleeting opportunities in harsh/unpredictable environments (common at low SES). This skill trades off against other executive functions.
Speciali-zation	Insecure attachment as determined by the Strange Situation (12 mos.).	Compared with securely attached children, better recall of negative events (e.g., spilling juice) but worse recall of positive events (e.g., receiving a birthday present) seen in a puppet show (3 yrs.; Belsky et al., 1996).	Enhanced recall of negative events promotes detection/avoidance of negative events in the future, which are more likely to occur in harsh family environments (as developmentally embedded through insecure attachment). This skill trades off against recall of positive events.
Speciali-zation	Low perceived or objective SES (at time of testing).	Enhanced response inhibition; better empathic accuracy; physiological responses and emotional contagion patterns more empathically linked to a	Enhanced empathic accuracy promotes behavioral prediction/management of external social forces/individuals that influence one's life outcomes (which

		social interaction partner (college and community adult samples; Kraus et al., 2012; Na & Chan, 2016).	occurs chronically for low SES individuals).
Speciali-zation	High risk from dangerous animals (birth to age at testing)	Enhanced learning about animal danger but not about dangers posed by material artifacts (ages 4-9 yrs.: Barrett et al., 2016).	Enhanced learning about dangerous animals promotes survival in environments where animal hazards are prevalent.
Speciali-zation	Institutional care; unpredictable/ unstable family environments (early childhood)	Enhanced performance on a risk-taking task that rewards exploitation (i.e., taking advantage of an immediate and small, but probable, reward; ages 6-15 yrs.; Humphreys et al., 2015); reduced effortful control (delay control) on a 'hot' task involving fleeting rewards, but not on a 'cool' task lacking an affective-motivational component (age 4 yr., 6 yr.: Sturge-Apple et al., in press).	Exploiting immediate rewards optimizes expected returns in unpredictable environments, where individuals have little control over future reward outcomes.
Speciali-zation	Harsh parenting (birth to 16 yrs., assessed retrospectively)	Enhanced deception detection in college sample; effect did not replicate in community sample (Frankenhuis, Roelofs, & de Vries, under review).	Increased deception detection reduces probability of morbidity, mortality, and exploitation in hostile family environment.
Speciali-zation/ Sensiti-zation	Maternal anxiety/ stress/depressive symptoms (prenatal; 3-24 mos. postnatal).	Enhanced psychomotor and mental development (3-24 mos. postnatal) when exposed to concordant prenatal and postnatal maternal depression (DiPietro et al., 2006; Sandman et al., 2012)	Matching hypothesis: Prenatal stress prepares the organism for stressful conditions later in life.
Speciali-zation/ Sensiti-zation	Severe neglect and/or abuse as determined by protective services (birth to age at testing).	Faster orientation to angry faces and voices; greater accuracy in identifying angry facial expressions from degraded stimuli; greater speed (but not accuracy) in identifying fearful faces (8-15 yrs.; Pollak, 2008; Pollak et al., 2009; Masten et al., 2008).	Faster and more accurate detection of threat promotes survival in hostile environments.
Speciali-zation/ Sensiti-zation	Child neglect; sexual and/or physical abuse as determined by protective services (birth to age at testing).	Heightened attention to and memory for negative, emotionally-laden or stressful information (Goodman et al., 2009); e.g., enhanced memory for a doctor who performed an invasive examination (3-16 yrs.; Eisen et al., 2007) or distracting aggressive stimuli (e.g., guns, swords) (4-9 yrs.; Rieder & Cicchetti, 1989).	Enhanced detection of and memory for threat promotes survival in hostile environments.

Sensiti-zation	High childhood unpredictability/ chaos (birth to 10 yrs.).[2]	Under primed conditions of economic decline/ uncertainty, enhanced attention-shifting ability but reduced inhibitory control (deliberate overriding of dominant responses) (college student samples; community sample: age 37; Mittal et al., 2015).	Enhanced shifting ability promotes detection of threats and taking advantage of fleeting opportunities in chaotic/unpredictable environments. Attention shifting trades off against inhibitory control.
Speciali-zation/ Sensiti-zation	High childhood unpredictability/ chaos (birth to 10 yrs., assessed retrospectively).	Under primed conditions of economic decline/ uncertainty, enhanced working memory in the form of rapid tracking and memory updating but reduced working memory in the form of long-term storage and information retention in the face of distraction (community adult samples; Young et al., 2016).	Enhanced rapid tracking and updating ability in working memory promotes the availability of current information, which is essential in chaotic/unpredictable environments, but trades off against longer term working memory functions.
Sensiti-zation	Low SES (at time at testing)	Under primed conditions of high financial demand, enhanced procedural learning (acquiring stimulus–response associations) but reduced performance on cognitive functions that rely heavily on working memory (college and community adult samples; Dang et al., 2016; Mani et al., 2013).	Enhanced procedural learning promotes acquisition of stimulus–response associations, which promote fast responding to environmental challenges (common at low SES), but trade off against working memory (DeCaro et al., 2008)

Note. SES: Socioeconomic status

[1]Resutls based on a middle-childhood sample (age at testing: 7-11 yrs.) and multiple college student samples.

[2]Childhood unpredictability was assessed retrospectively in the college student samples and prospectively in the community sample.