



Expectable environments in early life

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Humans develop in the context of environmental information that can be considered either experience-expectant or experience-dependent. Though the exact timing of sensitive period closures and consequences of environmental experiences have not been well delineated, early life is a period of increased vulnerability. While some forms of care (e.g. institutional care for children; representing the absence of experience-expectant caregiving) are not present in the evolutionary history of humans, it is likely that what is considered significant hardship today may have been more typical experience-dependent environmental information in the evolutionary timescale. Thus, assumptions that threatening or neglectful experiences are unexpected for the human child may not fit well in the scope of the broader timescale of human history. We argue that it is important to consider early caregiving experiences from the context of what has been expected in our evolutionary past rather than what is expected in modern sociocultural terms.

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The environmental information incorporated into building the developing brain can be categorized as experience-expectant or experience-dependent [1]. Theories of early adversity have noted that deviations from the expectable environment can have significant impacts on development, with the most devastating consequences occurring when experience-expectant information is missing in early life [2]. Evidence from studies on the effects of severe deprivation provides insight into the developmental time scale of these effects (i.e. sensitive periods) and inform our understanding of what are the fundamental expectations for the newest members of the

human species. Many expectations and associated responses develop over ontogenetic time as an infant experiences, and adjusts to, their unique environment. However, there is also an important set of shared expectations that have developed based on the environments humans were likely to encounter across phylogenetic time. While it is important to consider the precursors and foundations of adaptive functioning in today's environment, current research places a disproportionate emphasis on the experiences of individuals from WEIRD (Western, educated, industrialized, rich, democratic) cultures. This research base likely results in characterizations of an expected environment that may be misaligned with (species-typical) expectations. This may be particularly true when considering expectations of caregivers. Current research on the neurobiological and behavioral consequences of adversity, in particular, would benefit from applying a phylogenetic – not just ontogenetic – stance.

Early adversity as experience-expectant and experience-dependent deviations

The brain is theorized to be built through a combination of a genetic blueprint and environmental information [1]. This environmental information can be further categorized as either that which is expected to be encountered by all members of our species (e.g. exposure to light) or that which is dependent on idiosyncratic variation (i.e. not shared by all members of our species). The brain requires environmental input to be built, but also to specialize in the context cued by information unique to one's environment [3,4]. The idea that there is an expectable environment for human infants has been useful for providing a framework from which to consider the developmental impact of violations or deviations from what a human infant or young child may reasonably or typically experience [5]. For example, the insufficient care provided in orphanages (i.e. severe social neglect) is not typical for members of our species. Considering severe psychosocial deprivation as a deviation from the species-expectant environment has provided some utility for describing the severe impairments (i.e. reactive attachment disorder [6]) that appear to result from this type of experience, and highlights the experience of a responsive caregiving environment as species-expectant.

Variation in environmental information that is experience-dependent is also known to influence development. Both more common experiences of neglect (i.e. neglect not as severe as the severe psychosocial deprivation experienced in institutions), as well as physical abuse, are associated with a range of negative outcomes [7].

Theories on early adversity most commonly focus on these types of environmental input, with neglect considered a relative omission of appropriate care whereas abuse and other threatening experiences considered a commission of frightening/harmful care [8]. Typical processes related to learning about one's environment through experiences are believed to govern these responses to adversity, though there is also evidence for specificity at both the neural and behavioral levels. The effects of deprivation appear to result in reduced synaptic proliferation (particularly in the cortex) and the experience of deprivation is associated with performance on cognitive control tasks. Whereas, the effects of threatening experiences appear to affect emotion regulation circuitry and emotion processing [9,10*].

Yet, considering experience-dependent variation primarily from the perspective of adversity may artificially cut off what are likely to be continua by which to characterize individual environments. Research documenting the effects of variation in the early environment within the 'normative' range suggests that even caregiving differences found among volunteer parents from the community may result in meaningful differences in child brain structure and function [11–13]. Importantly, this challenges the idea that children simply require a species-expected 'good enough' environment [14]. Multidimensional characterizations of environmental variation in children's lives (e.g. considering both emotional and cognitive input on separate continua that range from neglect to enrichment, along with degree of sensitive caregiving received from one's primary caregiver) may be fruitful in determining the overlap among and potential differences in metrics of environmental experiences in early life [15*]. Further, this approach highlights that meaningful variation occurs not only with experiences of adversity, but also in the range considered 'good enough' as well as in highly enriched environments associated with human thriving.

What is the 'expected' environment?

Understanding the likely environments of humans on the phylogenetic scale may be useful for those interested in human responses to early experiences of adversity. Indeed, the argument has been made that creating a 'bridge' between evolutionary biology and developmental psychology can provide insight into potential natural selection pressures that might predispose us to exhibit certain behavioral responses observed today [16]. Most research linking adversity, broadly speaking, and later life outcomes has primarily taken a deficit approach. However, complementary approaches to examine potential strengths or 'hidden talents' among individuals as adaptations following exposure to adversity are also gaining attention [17,18,19*]. It is possible, and even plausible, that exposure to adversity can confer advantages under certain circumstances [20,21]. This concept of potential

adaptions to adversity that promote context-specific abilities is not an alternative to a deficit model and should be used as a complementary perspective in considering the effects of early experiences on functioning. Further, recent work found that the association between connectivity between specific brain networks and cognitive test performance was in opposite directions depending on whether children lived above or below the poverty line [22], suggesting the possibility of context-specific adaptations that predict functioning.

Given that the majority of research in developmental science is conducted with middle-class parent-child dyads from WEIRD societies [23], researchers obtain a limited view of the range of the early environment that may be expected by a member of our species. In other words, researchers considering variations in children's experiences may be overexposed, in relative terms, to highly responsive and child-centered care valued in WEIRD cultures [24]. Adverse caregiving and other environmental adversity may be less likely seen as aberrations of the human childhood experience when considered in the context of our evolutionary history. Fossil records of prehistoric children provide support that children worked in grueling physical conditions [25]. Threats not only from other humans, but also natural predators, likely resulted in a typical child in our past being exposed to frightening situations with greater regularity and with more serious consequences [26]. Historical records indicate a 27% mortality rate for infants, and that only approximately half of children lived to adulthood [27]. Comparatively, recent data from the U.S. indicate an infant mortality rate of less than .01%, and less than .02% from birth to adulthood [28]. Considering childhood and its expected environment from a historical lens may change our perceptions about what members of our species may have evolved to prepare for.

Sensitive period(s) for environmental information

In terms of *when* information about our environment is expected to be most influential, our limited evidence suggests that earlier, as compared to later, experiences of adversity have a more profound impact on developing brain circuitry [29]. During this time the brain is undergoing rapid development, not only of the limbic regions associated with emotion and memory, but also the prefrontal cortex, with evidence that experiences of both experience-expectant and experience-dependent deviations influence prefrontal cortex volume and connectivity (see Ref. [30*]). One study found that experience of sexual abuse at ages 3–5 years was associated with smaller hippocampal volume, though no association was found for sexual abuse occurring between the ages of 6–8 years [31]. Another study found that severity of stress from birth to age 5 years was associated with smaller hippocampal volume in early adolescence [32*], while no association was found between stressful experiences in later

childhood and hippocampal volume. Importantly, a growing body of research indicates that humans respond to variations in the environment much earlier than birth [33], highlighting that both prenatal and postnatal experiences shape brain development and subsequent behaviors.

Expectations from the caregivers' perspective

These findings on the possibility of a sensitive period highlight the observation that some degree of caregiver responsiveness in early life is an element of the evolved 'expected' environment from the infants' perspective. This highlights the need to consider what that means for what is expected of *caregivers*. Caregivers, and in particular, mothers, face considerable demands in caring for infants and young children. While evolutionary developmental psychologists tend to operationalize the likely fitness of offspring as a function of tradeoffs regarding parental options to either reproduce or conserve energy for their own growth (see Ref. [34]), it is possible that conservation could be seen in part through one's socio-emotional expenditure. For a parent, determining the costs and benefits of being an involved caregiver for an infant or young child may differ as a function of likely child mortality. Responsive and attentive caregiving for young children requires effort. In fact, declines in maternal sensitivity have been observed over the course of just 10 min of play with one's infant [35]. Reasonable concerns about the likelihood of loss of the child, paired with the considerable effort of attentive and responsive care, may promote strategies (whether conscious or unconscious) to limit emotional closeness in a manner that may be adaptive for caregivers (for modern examples see Ref. [36]). Psychological commitment to children is believed to be influenced by foster parents' concern that their foster child will be reunited with the child's biological parents [37]. Sociodemographic factors associated with the experience of stress and adversity (e.g. lower income, more children) are related to placing a relatively lower value on responsive and sensitive caregiving [38]. Thus, given closer consideration of our evolutionary timescale, in which loss and the experience of adversity were more prevalent than today, it may be that highly sensitive and responsive parenting is not the standard for our species. Assumptions that the natural tendency is for caregivers to be sensitive, and the associated implicit expectations placed on caregivers, may actually undermine prevention and intervention efforts aimed at improving the caregiving environment [39].

Conclusions

While non-human animal models can definitely assign causality in the relations between adversity and outcomes, a large body of longitudinal studies in humans indicate that early adverse experiences have widespread consequences on cognitive, social, and emotional functioning, with the most severe outcomes associated with

severe deprivation that violates experience-expectant caregiving and which occur earliest in life. Future research will benefit from a careful consideration of the types of early adversity and the timing of these experiences so that potential sensitive periods may be identified. Further, the degree to which different types of human experiences, including exposure to stressful, even life-threatening experiences, as well as caregiver insensitivity, may be less likely to be seen as significant deviations of the human experience when placed in the broader evolutionary context. What we consider adverse by modern standards could reflect a shift in perspective and expectations.

In applying the evolutionary-informed framework to understanding the expected environment, future research may be usefully guided by three overarching goals. First, with the understanding that our current conceptions of the 'ideal' caregiving environment may not be either culturally or phylogenetically sensitive, one goal must be to identify how to better assess and quantify the characteristics of a sensitive, responsive, and reliable caregiving environment and how that may vary both within and across different developmental contexts. A second goal must be to integrate developmental timing of brain plasticity, historical survival rates, and expectations for independence in childhood into future theory and analyses. Lastly, it will be imperative to determine how best to support the kinds of caregiving environments, particularly during foundational periods of development, that today we have evidence are associated with thriving. Assuming that caregiver sensitivity is what is 'natural' and expected may interfere with efforts to develop interventions to improve caregiving, and undermine those caregivers who might benefit most from intervention.

Conflict of interest statement

Nothing declared.

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