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Leveraging the developmental neuroscience of caregiving to promote resilience among youth exposed to adversity

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Abstract

Early adversity is a major risk factor for the emergence of psychopathology across development. Identifying mechanisms that support resilience, or favorable mental health outcomes despite exposure to adversity, is critical for informing clinical intervention and guiding policy to promote youth mental health. Here we propose that caregivers play a central role in fostering resilience among children exposed to adversity via caregiving influences on children's corticolimbic circuitry and emotional functioning. We first delineate the numerous ways that caregivers support youth emotional learning and regulation and describe how early attachment lays the foundation for optimal caregiver support of youth emotional functioning in a developmental stage-specific manner. Second, we outline neural mechanisms by which caregivers foster resilience—namely, by modulating offspring corticolimbic circuitry to support emotion regulation and buffer stress reactivity. Next, we highlight the importance of developmental timing and sensitive periods in understanding caregiving-related mechanisms of resilience. Finally, we discuss clinical implications of this line of research, and how findings can be translated to guide policy that promotes the well-being of youth and families.

Keywords

caregiver buffering; emotion socialization; corticolimbic circuitry; emotion regulation; early adversity

Introduction

Across development, caregivers play an outsized role in the emotional lives of children (Ainsworth, 1969; Bowlby, 1969; Lieberman, 2017), particularly in children's development of the capacity to regulate emotions (Calkins & Hill, 2007; Cassidy, 1994). Beginning at birth, stable caregiving is fundamental to children's emotional development (Hofer, 1978, 1994; Tottenham, 2012), and caregivers provide extrinsic scaffolding of children's

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increasingly emergent capacity to regulate their own emotions (Dozier et al., 2018; Gianino & Tronick, 1988; Hofer, 1994; Katz & Hunter, 2007; Pratt et al., 2015). Over time, and as caregivers adapt their behaviors to the child's changing needs, children undergo a shift from full reliance on caregivers to provide external regulation of their emotions in infancy to greater reliance on their own intrinsic capacity of self-regulation later in development (Grolnick et al., 2006; Thompson & Goodman, 2009). It is theorized that it is via this protracted socialization, which unfolds across development and occurs in tandem with fluctuations in other sources of social buffering, that caregivers influence their children's mental health and emotional well-being. The daily involvement of caregivers in their children's emotional lives directly influences children's development of psychobiological underpinnings of emotion regulation (Callaghan & Tottenham, 2016; Gee, 2016; Tan et al., 2020; Tottenham, 2015).

Though the role of parents in the emotional lives of children has universally important implications for child development across contexts (Morris et al., 2007), caregiving influences on the development of emotion regulation may have a particularly salient impact in the context of children's exposure to adversity due to the centrality of emotion regulation to processes of risk and resilience. Here we define resilience as positive mental health outcomes in the context of exposure to adversity; we consider resilience to be situated within a broader socioecological context and to be a dynamic and multifaceted process that is both influenced by and acts upon multiple systems (Masten et al., 2021). Emotion regulation, or an individual's ability to affect what emotions they experience, and when and how they experience and express these emotions (Gross, 1998), has been highlighted as a key transdiagnostic factor linking exposure to adversity and psychopathology (e.g., Ehring & Quack, 2010; Heleniak et al., 2016; Kim & Cicchetti, 2010; Villalta et al., 2018). Numerous studies have underscored that exposure to childhood adversity is linked with prototypically-maladaptive coping strategies (Compas et al., 2001)—for example, exposure to community violence, peer victimization, and parental loss are associated with higher levels of rumination (Heleniak et al., 2016, 2018; McLaughlin et al., 2009; McLaughlin & Hatzenbuehler, 2009), and meta-analytic findings have documented an association between maltreatment and lower levels of emotion regulation across domains, as well as increased reliance on prototypically-maladaptive strategies (Aldao & Christensen, 2015) such as avoidance and suppression (Gruhn & Compas, 2020). Despite demonstrated links between adversity exposure and reliance on potentially maladaptive emotion regulation strategies at a group level, empirical evidence supports that, on an individual level, prototypically-adaptive emotion regulatory processes following adversity may represent a mechanistic process of resilience. Across multiple cross-sectional and prospective samples representing youth exposure to a diverse range of adversities, reliance on maladaptive emotion regulation strategies and emotional reactivity have been found to mediate the association between youth exposure to trauma and the development of psychopathology (Heleniak et al., 2016; Kim & Cicchetti, 2010; Kim-Spoon et al., 2013; Weissman et al., 2019).

Here we propose that caregiving influences in the context of children's emotional lives—and on children's development of corticolimbic circuitry and emotion regulation—are a primary mechanism by which caregivers promote resilience following exposure to adversity. While the focus of the current review is on the role that caregivers play in children's emotional

lives, we note that there are numerous, interdependent ways that caregiver involvement in the lives of children influences children's responses to adversity—and therefore shapes processes of risk and resilience (see Williamson et al., 2017 for a review). For example, in the wake of exposure to adversity, caregivers have central roles to play in providing physical safety, establishing and maintaining routines, obtaining psychological treatment and medical care, and detecting risk to minimize exposure to subsequent trauma. Rather than being completely distinct caregiving influences, we view these as complementary and dependent on one another. For example, it is challenging for a caregiver to optimally support their child's emotional development when facing housing or food insecurity, limited access to resources, and ongoing threats to physical and psychological safety.

Within the context of a model by which children's brain and behavioral development mediates the association between adversity exposure and children's mental health, we examine the effects of caregiving on the link between adversity exposure and children's brain and behavioral development (i.e., a moderated mediation model; Figure 1). Here we conceptualize adversity broadly—including but not limited to physical abuse, sexual abuse, neglect, serious accidental injury, community violence, natural disaster, and forced displacement.

In the sections that follow, within the context of a model by which children's brain and behavioral development mediates the association between adversity exposure and children's mental health, we examine the effects of caregiving on the link between adversity exposure and children's brain and behavioral development (i.e., a moderated mediation model; Figure 1). Here we conceptualize adversity broadly—including but not limited to physical abuse, sexual abuse, neglect, serious accidental injury, community violence, natural disaster, and forced displacement. Specifically, we delineate how caregivers impact children's emotional functioning in the context of adversity from a multisystemic perspective—focused on behavioral, psychological, and neurobiological processes—and, further, synthesize evidence for associations between these processes and resilience following adversity. In addition, we review empirical work that has underscored important developmentally-specific effects of caregiving involvement in the emotional lives of children following adversity. We conclude by highlighting the importance of considering caregiving influences on children's emotional lives in both intervention and policy settings, which has critical implications for the well-being of youth exposed to adversity.

Mechanisms by which caregivers influence children's trajectories of resilience following exposure to adversity

A substantial body of literature has focused on caregiving influences on children's responses to trauma, highlighting several key ways that caregivers promote resilience via involvement in the emotional lives of offspring (Appleyard & Osofsky, 2003; Gewirtz et al., 2008; Williamson et al., 2017; Wilson et al., 2010). Drawing upon this literature, a meta-analysis of 14 studies comprising 4,010 participants that aimed to examine the impact of both positive and negative parenting practices on children's development of posttraumatic stress-related symptomatology following trauma exposure concluded that negative parenting

behaviors (e.g., hostility, overprotection) accounted for 5.3% of the variance in children's symptom development whereas positive parenting behaviors (e.g., warmth) accounted for 2% of the variance in children's symptom development (Williamson et al., 2017). These findings suggest that parents appear to exert a relatively small effect on children's mental health-related outcomes following adversity exposure, though the magnitude of these estimates is constrained by the focus of this meta-analysis on broad domains of parenting rather than more detailed mechanistic processes, as well as its focus on posttraumatic stress disorder (PTSD) as the sole clinical outcome of interest. Despite these constraints, these findings invite more detailed understanding of the specific ways in which parental involvement in the emotional lives of children in the wake of exposure to adversity has the potential to inform prevention and intervention efforts aimed at reducing the onset of trauma-related symptomatology. In the present review, we focus on several specific mechanisms by which caregiver involvement in the emotional lives of children following adversity may promote resilience. We highlight caregivers' attachment relationships with children as an ever-present basis of parental influences on child development in the context of adversity, and focus on caregiver promotion of generally benevolent environments and inputs in childhood, parental emotion socialization, including parental assistance with execution of specific emotion regulation strategies, and parental buffering of stress, as mechanisms by which caregiving is likely to influence children's developmental trajectories following exposure to adversity.

Child-caregiver attachment relationships as the basis of all caregiver influences

From birth, caregiver-child attachment relationships form the basis of a child's exploration of the world, and function as a critical lens through which children filter information about their environment and experiences (Bowlby, 1969). Secure attachment with caregivers facilitates caregivers' support of critical tasks of typical development (see Gee & Cohodes, 2021 for a review) (Figure 2). During infancy, children learn that primary caregivers are responsive to their needs and that caregiving behaviors are both predictable and associated with safety, with caregivers transitioning from being a source of comfort and protection to taking on more complex roles in facilitating infants' increasing exploration of their environment (Lieberman et al., 2015). During the transition to toddlerhood, caregivers continue to solidify their association with predictability and safety as children navigate strong—and at times conflicting—desires for both exploration and independence, as well as safety and security in their close contact with parents (Lieberman et al., 2015). Later, throughout early and middle childhood, caregivers scaffold children's exploration of physical and social environmental inputs as children develop increasingly complex schemas about the social and physical world, all while serving as a primary source of external regulation of children's emotions (Kopp, 1989; Morris et al., 2007). During the transition to adolescence, although the potency of caregivers' role as a source of external regulation wanes in some contexts as offspring become increasingly independent and other attachment figures (e.g., peers, romantic partners) begin to play a greater role in social buffering processes (Gee, 2016; Hostinar et al., 2014), caregivers continue to play important roles in socializing coping behaviors and guiding adaptive behavior (Butterfield et al., 2019; Rogers et al., 2020).

In this developmentally salient and evolving manner, caregiver-child attachment relationships form the backdrop of children's increasing exploration, independence, and accomplishment of tasks of development. These processes are ubiquitous in both typical development and in the context of adversity, and evidence suggests that caregivers leverage attachment relationships to promote resilience following exposure to adversity, with the quality of a child's attachment largely governing caregivers' capacity to support children following adversity exposure (Lieberman, 2004; Lieberman, Van Horn, et al., 2005; Lieberman et al., 2011; Lieberman & Pawl, 1988). Further, recent theoretical work highlights that specific patterns in caregiving behavior—namely the co-occurrence of predictability and safety—may be particularly salient inputs during infancy and toddlerhood, and may prime a caregiver's ability to serve as a source of external regulation later in development by directly impacting neural circuitry supporting emotion regulation (Gee & Cohodes, 2021b). We argue that these critical elements of caregiving in the earliest periods of development not only facilitate optimal caregiver inputs in infancy and toddlerhood but also enable ideal input from caregivers across development. In the context of exposure to adversity, caregivers are likely to be able to take advantage of prior establishment of themselves as predictable—and as harbingers of safety—to facilitate greater parental attenuation of the impact of adversity via the numerous pathways described below.

One outstanding question pertains to the degree to which aversive caregiving has the potential to undermine parental influences on children's recovery following adversity. As exposure to any form of trauma can influence nearly all aspects of children's functioning and development, and result in broad set of beliefs and altered cognitions regarding a generalized lack of safety in the world, children's exposure to both trauma that involves a caregiver in a perpetrating role (e.g., perpetration of maltreatment, neglect) and trauma that does not directly involve a caregiver (e.g., medical trauma, natural disaster) has the potential to “shatter the protective shield” of parental attachment (Lieberman & Amaya-Jackson, 2005). For example, even when caregivers do not perpetrate trauma, children may come to view their caregivers as inconsistent or unpredictable sources of protection and safety in the context of a risky environment and therefore, caregiver-child attachment relationships—the very mechanism by which parents support children in the aftermath of adversity—may be compromised by adversity (Bernstein & Freyd, 2014).

However, the degree to which adversity in the context of the caregiver-child relationship disrupts a child's orientation to a caregiver as a source of stability and safety may vary by developmental stage. Specifically, there is increasing evidence that, in the earliest stages of development, offspring prefer cues related to their caregivers, even when these cues have an inherently aversive quality. This absence of avoidance learning is believed to facilitate formation of attachment relationships even in the context of adversity (Gee, 2020; R. Perry & Sullivan, 2014). Specifically, young children were more likely to approach conditioned stimuli acquired in the presence of their caregiver, and, conversely, to avoid stimuli acquired in the absence of their caregiver (Tottenham et al., 2019). These findings directly parallel evidence from the rodent literature that offspring approach aversive stimuli when paired with a maternal cue during a period of development when maternal presence dampens affective reactivity in rodent offspring (Moriceau & Sullivan, 2006). This pronounced attraction to caregiver-related cues—even in the context of adversity—in the earliest stages

of development may facilitate attachment and promote close physical proximity between caregivers and offspring despite adversity. The degree to which this pattern has broad ecological validity to a range of trauma exposures and across development remains unclear, and failure to establish safety and predictability in the context of caregiving relationships in infancy and toddlerhood may alter the degree to which caregivers can enact optimal influences on children's emotional lives later in development, particularly in the context of adversity (Gee & Cohodes, 2021b; R. Perry & Sullivan, 2014).

Caregiver promotion and maintenance of broadly benevolent childhood environments and predictable routines in the context of family life

One primary way in which caregivers may promote resilience is via the establishment and maintenance of a home environment that yields beneficial inputs for children following adversity. In addition to extensive empirical work highlighting associations between childhood adversity and the development of psychopathology, substantial work has highlighted broad and general promotive childhood experiences that may mitigate the impact of adversity (Crandall et al., 2019, 2020; Narayan et al., 2018; Wright et al., 2013). In a major study assessing the impact of benevolent childhood experiences on later development of trauma-related psychopathology, endorsement of a higher number of benevolent childhood experiences (e.g., having good neighbors, having an opportunity to have fun) was found to be associated with lower levels of psychopathology and, critically, to offset the impact of adverse childhood events on the development of psychopathology later in life (Narayan et al., 2018). These findings, based on the establishment of the Benevolent Childhood Experiences (BCEs) Questionnaire (Narayan et al., 2018), are in line with previous evidence that parental maintenance of a positive home environment—and broad and general promotive and protective factors—are a primary mechanism by which caregivers support children's resilient functioning in the context of exposure (e.g., Collishaw et al., 2007; Doom et al., 2021; K. Howell et al., 2010; Morris et al., 2021), possibly via the impact of positive parenting practices and beneficial environments on children's symptomatology via promotion of children's emotion regulation (K. Howell et al., 2010).

One particular element of family environments that has received considerable attention is caregiver maintenance of consistent home routines and practices, yielding a sense of predictability for youth (Greeff & Wentworth, 2009; Williamson, Hiller, et al., 2018). Caregiver maintenance of family routines following children's exposure to adversity has been linked to reduced child symptomatology (Boyce, 1981; Foy, 1992). Extending this work to the COVID-19 pandemic, a predictable home environment buffered the impact of exposure to COVID-19-related stress on children's mental health during the pandemic (Glynn et al., 2021), with parental maintenance of family routines also emerging as a specific moderator of the association between exposure to COVID-related stress and youth symptomatology (Cohodes, McCauley, et al., 2021) and family-level resilience (Bates et al., 2021). Though additional empirical work is required to elucidate specific mechanisms by which predictable home routines confer resilience during or following exposure to adversity, it is possible that predictable home routines signal predictable caregiver involvement in the emotional lives of children—as sources of external emotion regulation and active

participants in the daily socialization of emotion—and therefore exert influences on child symptomatology via promotion of child regulation.

Caregiver socialization of children's emotions

Gottman's parental meta-emotion philosophy (Gottman et al., 1996) proposes that caregivers' beliefs about their children's emotions—including the degree to which they are aware of, accepting of, and directly involved in coaching their children's emotions—manifests in behavioral responses to children's displays of negative emotions. Parental meta-emotion philosophy has been found to predict numerous outcomes in offspring, including the development of psychopathology (see Gottman et al., 1997 for a review). In the context of adversity exposure, parental emotion coaching, in particular—or the degree to which parents engage in assisting their children in identifying the emotions they are experiencing, show respect for their children's emotions, and actively engage in assisting children cope with emotion-eliciting situations (Gottman et al., 1996, 1997)—has been highlighted as a buffer of children's development of symptomatology following exposure to a range of stressors (Cohodes et al., 2017; Cohodes, McCauley, et al., 2021; Fogarty et al., 2019; Greene et al., 2020; V. Johnson & Lieberman, 2007; L. Katz et al., 2015; L. F. Katz & Windecker-Nelson, 2006), including exposure to COVID-related stress in the context of a global pandemic (Cohodes, McCauley, et al., 2021; Lobo et al., 2021). Of note, additional empirical work suggests that parental emotion awareness, acceptance, and coaching appear to affect children's outcomes following exposure via encouragement of children's own intrinsic emotion regulation capacities in the context of negative emotion (B. H. Ellis et al., 2014; Wu et al., 2020). These findings—suggesting a primary mechanism by which caregiver involvement in the emotional content of a stressor may impact children's behavior, and, resultingly, children's development of trauma-related symptomatology—are consistent with prominent etiological models of childhood PTSD highlighting caregivers' capacity to affect children's tendency to engage in negative reappraisals of the event and use of maladaptive coping and regulation strategies (Cobham et al., 2016; Ehlers et al., 2003; Ehlers & Clark, 2000; Meiser-Stedman, 2002; Stallard & Smith, 2007; Williamson et al., 2016). For example, a longitudinal empirical investigation of children's mental health following natural disasters demonstrated that parent-child interactions characterized by negative parental appraisals of a traumatic event, as well as promotion of avoidant coping behaviors, was associated with increased child symptomatology, and further, suggest that this association is likely driven by the effect of parental appraisals and coping responses on children's development of their own maladaptive coping strategies (Hiller et al., 2018).

Highly related to parental emotion coaching, parental availability for discussion of stressful events may attenuate the impact of adversity exposure on children's development of symptomatology (Carpenter et al., 2017; Cohodes et al., 2021; Stallard et al., 2001). Parents who report providing children with frequent opportunities to discuss their feelings about recent stress exposure in an age-appropriate manner may buffer children's development of stress-related psychopathology via direct impacts on the valence of a child's appraisal of an event (Williamson, Halligan, et al., 2018; Williamson, Hiller, et al., 2018). In addition, parents may affect the content of children's narratives about their adversity exposure

(Fivush et al., 2003), in the service of buffering harmful impacts of adversity on children's development of symptomatology (Kilmer & Gil-Rivas, 2010).

Recent advances in measurement of caregiver emotion socialization (Cohodes, Preece, et al., 2021) have facilitated assessment of the degree to which caregivers support children's emotion regulation at the strategy-specific level. In the context of exposure to stress, a recent study examined parental assistance with prototypically-adaptive and maladaptive emotion regulation studies as a potential moderator of the impact of family-level COVID-related stress exposure on children's development of internalizing and externalizing symptomatology. Results suggest that caregiver assistance with prototypically-adaptive emotion regulation strategies (i.e., acceptance) buffered the impact of exposure to COVID-related stress, while assistance with prototypically-maladaptive strategies (e.g., rumination) exacerbated its impact (Cohodes et al., 2022). Though this line of work is emerging, the impact of caregiver emotion socialization on children's mental health in the context of adversity exposure likely varies by the specific emotion regulatory processes that caregivers support.

Neurobiological mechanisms associated with caregiving influences on children's emotional functioning

A growing literature in developmental neuroscience has identified neurobiological processes by which caregiving influences children's emotional functioning (Callaghan & Tottenham, 2016; Farber et al., 2022; Gee, 2020; Tan et al., 2020; Tottenham, 2020), providing mechanistic insight into the ways that caregivers promote resilience following adversity. Affective learning and regulation are broadly supported by corticolimbic circuitry, which involves connections between the prefrontal cortex and subcortical structures involved in emotion processing (Kovner et al., 2019). Among key regions in this circuitry, the amygdala plays a central role in detecting emotionally salient stimuli in the environment and in guiding behavior in response to affect. The hippocampus is involved in emotional learning and memory. The medial prefrontal cortex is critical for regulating the amygdala and emotional reactivity. Paralleling dynamic changes in emotion processing across childhood and adolescence, this circuitry undergoes protracted development (Bloom et al., 2022; Casey et al., 2019; Gee et al., 2018; Hare et al., 2008).

Cross-species evidence shows that caregivers influence the development of corticolimbic circuitry, with an especially prolonged period of influence in humans (Callaghan et al., 2014; Tottenham, 2015). While studies of youth exposed to caregiving-related adversity have contributed some of the strongest evidence of caregiving influences on neurodevelopment (Nelson & Gabard-Durnam, 2020; Sheridan et al., 2012; Tottenham, 2012), a growing literature has pointed to associations between typical variation in caregiving behaviors and offspring brain development (Farber et al., 2022; Tan et al., 2020). Many of these studies have focused on aspects of caregiving related to warmth (versus harshness or hostility) and sensitivity (i.e., the extent to which a caregiver is attuned and responsive to their child). During childhood, caregiver sensitivity is associated with amygdala volume and microstructure of the amygdala and hippocampus (A. Lee et

al., 2019), and negative caregiving behavior is associated with amygdala activation and functional connectivity to affective stimuli (Pozzi et al., 2019). In addition, maternal hostility and regulation at age 3 were associated with children's corticolimbic function at ages 7-8 (Kopala-Sibley et al., 2020), suggesting that caregiving in the earliest years of development may prime the development of corticolimbic circuitry. During adolescence, findings suggest sustained impact of caregiving behaviors. For example, parental warmth and support were associated with lower amygdala reactivity to fearful faces among adolescents (Romund et al., 2016), and harsher parenting was associated with reduced ventrolateral prefrontal engagement during peer rejection among adolescents at risk for anxiety disorders (Guyer et al., 2015). Evidence suggests these associations between caregiving and brain function have important implications for mental health. Among adolescents, higher parental warmth was associated with lower symptoms of anxiety and depression two years later via effects on subgenual anterior cingulate activation (Butterfield et al., 2020). Together, these findings suggest that harsher parenting is associated with weaker prefrontal control in certain contexts requiring regulation (e.g., Guyer et al., 2015), whereas caregiver warmth and sensitivity are generally associated with lower reactivity in regions such as the amygdala in negatively valenced contexts (e.g., Kopala-Sibley et al., 2020; Pozzi et al., 2019; Romund et al., 2016), as well as lower internalizing symptoms (e.g., Butterfield et al., 2020).

Regulatory influences: Caregiver buffering of neural function and behavior

Consistent with the idea that caregivers can promote resilience by influencing the neurobiological processes supporting regulation, evidence suggests that supportive caregiving can buffer the effects of numerous types of adversity on HPA axis function, corticolimbic circuitry, and epigenetic aging (Brody et al., 2016, 2019; Brown et al., 2020; Gunnar & Donzella, 2002; Kahhalé et al., 2023; Stevens et al., 2021; Whittle et al., 2017). Paralleling evidence that caregivers play a central role in guiding children's emotional learning (Tottenham et al., 2019; van Rooij et al., 2017) and helping to regulate children's emotions and stress (Cohodes et al., 2017; Cohodes, McCauley, et al., 2021; Compas et al., 2001; Eisenberg et al., 1998), cross-species research has provided evidence that caregivers serve an external regulatory function as corticolimbic circuitry is developing (Callaghan & Tottenham, 2016; Gee et al., 2014; Gee, 2016; Gunnar & Donzella, 2002; Hofer, 1994; C. L. McCoy & Masters, 1985). Consistent with findings in rodents and macaques (Moriceau & Sullivan, 2006; Sanchez, 2006), research in humans has shown that caregiver presence can buffer children's responses to stress by dampening cortisol reactivity (Hostinar et al., 2015) and amygdala reactivity (Gee et al., 2014). In a study of caregiver buffering at the neural and behavioral levels, children and adolescents performed an emotional go/no-go task of inhibitory control in an affective context twice in the laboratory, once in the presence of their mother and once in the presence of a stranger. During an fMRI scan, participants viewed faces of their mother and of a stranger. Consistent with parental regulation of behavior, children showed better inhibitory control (i.e., fewer false alarms) when seated next to their mother than a stranger in the laboratory. Children showed lower amygdala reactivity when viewing their mother's face than when viewing a stranger's face. Moreover, exposure to the mother's face, relative to the stranger's face, phasically induced a pattern of stronger inverse mPFC-amygdala functional connectivity that is typically observed at older ages and that has been associated with greater regulation in prior work (e.g., Banks et al., 2007). In

this study, caregiver buffering at the neural level was associated with individual differences in behavior, such that children whose parents buffered more strongly at the neural level exhibited better inhibitory control in their parent's presence (Gee et al., 2014). Of note, the effects of caregiver buffering observed in this study were specific to childhood and were not evident for adolescents in this study, which may be indicative of a relatively reduced dependence on external regulation in some affective contexts during adolescence. Together, these findings suggest that modulation of the HPA axis and frontoamygdala circuitry is one primary way that caregivers confer external regulation while regulatory systems are still developing during childhood.

Despite increasing independence from their caregivers as youth mature, caregivers continue to play an important role in scaffolding regulation during adolescence. However, at both behavioral and neural levels, the nature of this role appears to change in a manner consistent with the developing skills and unique needs of adolescents (Telzer et al., 2018). Demonstrating the prevailing role of parents in guiding offspring behavior via external regulation in adolescence—and the potentially increased importance of parents in appetitive social contexts that may induce a propensity for risk taking, a series of studies has shown that the presence of a parent can redirect adolescents toward safer behavior and stronger regulation in rewarding social contexts (Guassi Moreira & Telzer, 2018; Qu et al., 2015; Rogers et al., 2020; Telzer et al., 2015). As one example, compared with younger youth, older youth showed more disinhibition toward appetitive than aversive stimuli in social contexts. However, parental presence buffered this effect, such that there was no age-related difference when the parent was present (Rogers et al., 2020). With increasing age, adolescents exhibited greater vmPFC activation and frontoamygdala connectivity in socially appetitive contexts when in their parent's presence, suggesting a prefrontal mechanism supporting the regulatory effects of caregivers during adolescence. In addition to the buffering effects of caregiver presence, caregivers appear to support adolescents' emotional well-being by socializing coping behaviors (e.g., A. S. Anderson et al., 2021; Liga et al., 2020). Building upon this behavioral literature, a recent study found that parental socialization of coping behaviors modulates adolescent mental health via modulation of neural circuitry implicated in affective regulation. Specifically, parents' use of reframing and problem-solving statements during a parent-adolescent interaction was associated with adolescents' insula and perigenual cingulate activation in response to affective stimuli. Among adolescents with anxiety disorders, parents' socialization of prototypically-adaptive coping strategies was associated with lower use of disengaged coping in adolescents' daily life via these patterns of neural activation (Butterfield et al., 2019). Together, these findings suggest that adolescence may be an especially important time for caregivers' scaffolding of adaptive coping and safe behavior in the context of social challenges, which commonly arise in more appetitive contexts, during adolescence.

Ontogeny of caregiver buffering and individual differences

Understanding how caregiving cues facilitate regulation—and how these experiences become biologically embedded to influence the development of children's intrinsic regulatory capacity—can provide insight into the ways that caregivers foster resilience following adversity. We have previously proposed that effective caregiver buffering

requires the pairing of predictability and safety in children's experience of caregiver cues (Gee & Cohodes, 2021b). Specifically, children's interactions with caregivers provide opportunities to experience caregiver buffering and to learn about the degree to which their caregiver's presence is associated with the attenuation of fear (Gee et al., 2014; Moriceau & Sullivan, 2006). Through these repeated interactions, consistent—and predictable—experiences of caregiver regulation (e.g., via physical presence and related attenuation of physiological reactivity; (Callaghan & Tottenham, 2016) reinforce the association between caregiver presence and safety. A growing body of cross-species evidence indicates that the predictability of caregiving signals acts on corticolimbic circuitry (Glynn & Baram, 2019), with demonstrated effects on mPFC-amygdala connectivity (Granger et al., 2021; Guadagno et al., 2018) and amygdala reactivity (Malter Cohen et al., 2013). Across time, repeated co-activation of the amygdala and mPFC via parental presence may contribute to the development of this circuit and internalization of regulatory capacities (Callaghan & Tottenham, 2016; Gee, 2016). Evidence in humans shows that frontoamygdala connectivity to affective stimuli predicts frontoamygdala connectivity at rest two years later, suggesting that repeated co-activations during development may shape the more stable architecture of this circuit later in life. Indeed, environmental experiences that co-activate regions within a circuit can shape long-term changes in connectivity during adulthood (L. J. Gabard-Durnam et al., 2016; Kelly & Castellanos, 2014), which may be especially likely for early caregiver influences given heightened neuroplasticity and neural sensitivity to caregiving experiences early in development. Over time, such neurobiological scaffolding may be a mechanism by which the external regulation provided by caregivers becomes internalized as youth mature and become more independent.

Although group-level effects of caregiver modulation of offspring neural function and regulatory behavior have been identified during childhood and adolescence, there is important variability in these effects across individuals. Consistent with the idea that early caregiver-child attachment lays the foundation for subsequent caregiving influences on children's emotional functioning (Sroufe, 2005), individual differences in caregiver buffering have emerged as a function of attachment security in several studies. Specifically, children who reported greater security in their relationship with their caregiver showed greater caregiver-related attenuation of amygdala reactivity (B. Callaghan et al., 2019; Gee et al., 2014). In addition, in a study of adolescents, attachment history (i.e., attachment classification assessed during early childhood) moderated the effects of caregiver presence on regulatory behavior and neural functioning in response to affective cues, such that the buffering effect of caregiver presence was stronger among adolescents with a history of insecure attachment (relative to those with a history of secure attachment) (Rogers et al., 2021). While future work is needed to better understand the relation between attachment and caregiver buffering across a range of contexts and developmental stages, broadly, these findings reinforce that individual youth are differentially sensitive to caregiving experiences (e.g., Schriber & Guyer, 2016) and highlight the importance of considering individual differences in the nature of caregiver-child relationships. Namely, children's individual profiles of caregiving adversity (e.g., frequency and chronicity of disrupted attachment relationships, history of caregiver betrayal) are likely to directly inform individuals' capacity

to optimally benefit from caregivers' external regulation, which may have important implications for the development of psychopathology following adversity.

Caregiver buffering following adversity

Consistent with the idea that early experiences with caregivers may shape subsequent experiences of social buffering (Gee & Cohodes, 2021b; Hostinar et al., 2014), across species, early caregiving adversity is associated with weaker effects of caregiver buffering later in development across species. Even though the evolutionary drive to establish attachment relationships persists even in the context of threatening cues (R. Perry & Sullivan, 2014), animal studies demonstrate that caregiving adversity interferes with caregiver buffering. Specifically, pups exposed to maternal maltreatment (e.g., rough handling of pups, stepping on pups) do not show the expected pattern of suppression of fear-related behavior in the presence of their mother during infancy, and, further, did not appear to benefit from maternal buffering to the same degree as their non-maltreatment exposed counterparts during the adolescent period with regard to their fear-related behavior (Opendak et al., 2019; Robinson-Drummer et al., 2019). Similarly, among non-human primates, infant maltreatment is associated with less effective maternal buffering of cortisol reactivity (Sanchez et al., 2015). In the context of human development, a recent study examined caregiver buffering of amygdala reactivity among youth who were previously exposed to caregiver deprivation via institutionalized care and later adopted into stable families. Findings suggest that, on average, children exposed to caregiver deprivation early in life do not benefit from caregiver buffering of amygdala reactivity (Callaghan et al., 2019). However, there is substantial variability in this effect and 40% of youth who previously experienced caregiving-related adversity *did* show reduced amygdala reactivity to caregiver cues. Paralleling findings related to individual differences in responses to caregiver buffering in typical development (i.e., among youth who did not experience caregiving adversity), greater caregiver-child attachment security was associated with stronger caregiver buffering of amygdala reactivity (Callaghan et al., 2019). Importantly, youth who appeared to respond to caregiver buffering despite a history of caregiving adversity also had lower levels of anxiety-related symptomatology up to three years later, suggesting that caregiver buffering of amygdala reactivity may be a mechanism by which caregivers promote resilience among youth at elevated risk of psychopathology due to their exposure to adversity.

Moreover, these findings highlight malleability in buffering effects following early caregiving disruptions. Despite the absence of consistent safety-related caregiving cues in the first few years of life, children exposed to early caregiver adversity who showed caregiver-related attenuation of amygdala reactivity benefited from having learned to associate their adoptive caregivers with safety during a later developmental stage (B. Callaghan et al., 2019). Consistent with this idea, evidence from rodent studies shows that exposure to subsequent augmented caregiving following caregiving-related adversity is associated with neurodevelopmental changes that support adaptive responses to stress (e.g., Singh-Taylor et al., 2018). Thus, although optimal patterns of early caregiver inputs may prime corticolimbic circuitry to be more receptive to caregiver modulation later in life, high-quality care following adversity may foster plasticity in youths' capacity to benefit

from subsequent caregiver buffering. Consistent with these ideas, in our conceptual model, caregiving influences can indeed stem from caregivers who have been associated with adversity. In the context of caregiving-related adversity, there is more likely to be disruption in the extent to which a child associated a caregiver with safety and predictability (Gee & Cohodes, 2021). Thus, benevolent influences of a caregiver who previously perpetrated adversity or was associated with adversity are more complicated than caregiver influences that have consistently been associated with safety and predictability. However, often with significant support and intervention (Lieberman & Van Horn, 2008), the potential for buffering and benevolent caregiving experiences still exists.

The role of developmental timing of adversity exposure and sensitive periods in caregiving influences

Dynamic changes in plasticity and neurodevelopment across childhood and adolescence have broad implications for how caregiving experiences shape children's emotional functioning and foster resilience following adversity. During sensitive periods of heightened plasticity, the brain is more amenable to environmental influences (Knudsen, 2004; Werker & Hensch, 2015) and experiences can lead to a series of developmental cascades that can have downstream effects—both positive and negative—on mental health (Davidson & McEwen, 2012; Masten & Cicchetti, 2010). Such periods can render children particularly vulnerable to caregiving disruptions, but can also confer unique opportunities for intervention and buffering effects of augmented caregiving (Gee & Casey, 2015).

Cross-species evidence suggests that the period spanning infancy and toddlerhood may represent a sensitive period during which caregiver inputs that are predictable and associated with safety may be particularly important for establishing a foundation for later caregiver modulation of corticolimbic circuitry and emotional functioning (Figure 2). The absence of stable, nurturing caregiving early in life disrupts corticolimbic development across species. For example, early caregiver deprivation is associated with altered connectivity between the amygdala and mPFC in mice (F. K. Johnson et al., 2018), rats (Yan et al., 2017), non-human primates (B. R. Howell et al., 2019), and humans (Gee et al., 2013) (others). Disruptions to stable, supportive caregiving have particularly strong influences when they occur early in life, relative to later stages of development (Nelson & Gabard-Durnam, 2020; Tottenham, 2012), suggesting that this developmental period may reflect a sensitive period driven by experience-expectant mechanisms. Some of the strongest evidence for an early sensitive period related to species-expected caregiving comes from the Bucharest Early Intervention Project (BEIP), a randomized controlled trial that randomly assigned children in institutionalized care to either be placed in foster care or to remain in institutionalized care (Nelson et al., 2007). Findings suggest that youth exposed to caregiver deprivation in the context of institutionalized care show more secure attachment, more normative stress responses, and more normative neurodevelopmental trajectories following placement into a foster care intervention prior to 24 months of age, relative to peers who were placed after 24 months of age (McLaughlin et al., 2011, 2015; Vanderwert et al., 2016). While studies of caregiving disruptions in humans involve complex adversities (e.g., parental deprivation, maltreatment) characterized by both the absence of species-expected inputs and

the presence of extreme stress (which may, themselves, alter the timing of sensitive periods [see Gabard-Durnam & McLaughlin, 2020 for a review]), this evidence suggests that the first two years of life may be a potential sensitive period during which the absence of key aspects of species-expected caregiving inputs—such as the repeated co-occurrence of predictability and safety—may exert a particularly strong effect on neurodevelopment and longer-term emotional functioning.

Emerging evidence suggests that adolescence may represent another developmental window with increased potential for positive influences of supportive caregiving. Adolescence is a unique period for neurodevelopment and socioemotional functioning, with a broad array of challenges and opportunities (Andersen, 2003; Fuhrmann et al., 2015; F. S. Lee et al., 2014; Sisk & Gee, 2022). Despite exposure to increased stressful life events and the onset of many stress-related psychiatric disorders during adolescence (Kessler et al., 2005; McLaughlin et al., 2012), adolescents may be especially poised to benefit from positive caregiver influences following early-life adversity. As one example, a recent study using longitudinal data from the BEIP identified adolescence as a period of heightened sensitivity to the caregiving environment (Colich et al., 2021). Higher caregiving quality in adolescence was associated with greater reward responsivity and executive functioning, as well as lower internalizing and externalizing problems; further, these associations were strongest at age 16, relative to ages 8 and 12. These findings suggest that positive caregiving experiences during adolescence may be especially helpful to promote resilience among children exposed to earlier adversity and complement recent evidence that stress response systems may undergo a period of increased plasticity during adolescence. Specifically, adolescents who experienced caregiver deprivation early in life but were later adopted into stable families showed evidence of recalibration of the HPA axis with pubertal development (DePasquale et al., 2019, 2021; Gunnar et al., 2019). As such, increased plasticity of the HPA axis during adolescence may promote recalibration to current environmental inputs, such that supportive caregiving environments may have an outsized impact on psychobiological development during this period. Of note, the role of pubertal recalibration on the longer-term development of socioemotional processes is not yet fully understood and recent longitudinal analyses suggest that recalibration may actually be associated with poorer long-term adjustment (N. B. Perry et al., 2020, 2022). Future research will be important to further examine the optimal nature of an adolescent environment that facilitates recalibration, as well as its potential neural and behavioral consequences.

In addition to the role of developmental timing itself in the effects of adversity and caregiving experiences (Gee & Casey, 2015; Lupien et al., 2009; McCrory et al., 2013; Sabatini et al., 2007; Teicher et al., 2016; Tottenham & Sheridan, 2009), developmental timing intersects with key features of experience to shape neurodevelopment and emotional functioning. The extent to which a caregiver is involved in children's experiences of adversity—whether through connection to the adversity itself or through supporting children's coping in its aftermath—is likely to be especially impactful during developmental periods of heightened sensitivity (Cohodes, Kitt, et al., 2021; Gee & Casey, 2015). Caregivers may be involved in adversity exposures in a variety of ways, including via direct involvement (e.g., caregiver perpetration of abuse or neglect) or parent-child dyadic exposure to adversity (e.g., shared exposure to domestic violence). Exposure to adversity

that involves deviations from species-expected caregiving (e.g., caregiver perpetration of maltreatment) has the potential to disrupt the caregiver-child attachment relationship and to hinder the efficacy of caregiver buffering following adversity (Lieberman, 2004). Consistent with this idea, several studies have found that, relative to children exposed to non-caregiver-related adversity, children who experienced caregiver-related adversity showed greater symptomatology, as well as difficulties with affect regulation and interpersonal relationships (Cook et al., 2005; D'Andrea et al., 2012). In addition, in this vein, children exposed to adversity characterized by maladaptive family functioning were more likely to develop mental health problems than children exposed to adversities not characterized by maladaptive family functioning (McLaughlin et al., 2010). These findings have important implications for the ways that caregivers might support children's emotional functioning following exposure to adversity and highlight the importance of interventions that support families with ongoing threats to caregiving relationships or in which a caregiver's own traumatic exposure affects their capacity to be involved in children's emotional functioning in an adaptive way. Given the essential role of attachment in development and emotional functioning (Bowlby, 1969; Cassidy & Shaver, 2002), such caregiver-involved adversity may have an especially pronounced impact on mental health in childhood, and delineating interactions between the timing of adversity and features such as caregiver involvement may directly inform interventions (Cohodes, Kitt, et al., 2021).

Implications for treatment

Here we propose that caregivers' engagement with children's emotional development is a primary mechanism by which caregivers promote children's resilience in the context of adversity. Further, attachment relationships form the basis of the numerous specific ways in which caregivers exert this influence across development (Sroufe, 2005). Given the potential for adversity exposure to negatively impact attachment relationships, exposure to adversity may undermine the very caregiving influences that have the potential to buffer children from the deleterious sequelae of these exposures (Lieberman & Amaya-Jackson, 2005). Therefore, bolstering caregiver-child attachment relationships—and, in turn, a caregiver's ability to support children's emotion regulation—is a key treatment target for youth exposed to adversity (Dozier et al., 2018; Lieberman, Van Horn, et al., 2005). Relational interventions such as Child-Parent Psychotherapy (CPP; Lieberman et al., 2005), Trauma-Focused Cognitive Behavioral Therapy (TF-CBT; Cohen et al., 2000; Cohen et al., 2011), the Child and Family Traumatic Stress Intervention (CFTSI; Berkowitz et al., 2010), Parent-Child Interaction Therapy (PCIT; Thomas & Zimmer-Gembeck, 2012), and Attachment-Based Family Therapy (ABFT; Diamond et al., 2012) that center dyadic processes between caregivers and children, and focus on restoring optimal caregiving inputs for children following adversity (e.g., establishment or reestablishment of safety in the context of family life) are likely to promote children's ability to benefit from caregiving in the context of trauma (e.g., Lieberman et al., 2005; Lieberman & Van Horn, 2011). Importantly, the appropriate relational intervention program will ultimately depend on a particular child's history of adversity exposure—and the past and current family context—and will be influenced by factors such as whether caregivers have engaged in maltreatment or neglect.

Consistent with the increasing emphasis on precision medicine-based approaches to selecting and individualizing psychotherapeutic interventions for youth and families exposed to adversity (Aschbacher et al., 2022), delineation of the ways that children's specific profiles of adversity exposure and developmental stage relate to emotional learning and regulation are likely to inform optimized and individualized approaches to intervention (Gee et al., 2022) (Figure 3). For example, interventions can be tailored based on an individual's profile of exposure to adversity across multiple dimensions (Cohodes, Kitt, et al., 2021; Cohodes et al., 2023; Nikolaidis et al., 2022), based on specific patterns of caregiver-child interactions (Kitt et al., 2022), or based on specific caregiver-level factors such as parental symptomatology following dyadic exposure to adversity (Hagan et al., 2017). We specifically highlight the importance of considering family-level processes in treatment selection and optimization given the multifaceted influence of caregivers on resilience-related processes reviewed here (Garner et al., 2021). While variability in numerous factors could lead to diverse characterizations of an individual's exposure to adversity and their caregiving experiences, the following dimensions may be especially important for understanding the optimal role of caregivers in promoting youth's resilience and optimizing interventions to support caregiving influences: a) adversity: extent to which a caregiver was involved in adversity, extent to which adversity was characterized by threat, deprivation, or unpredictability, developmental timing of the adversity; b) caregiving: extent to which caregiver is associated with safety or predictability, caregiver warmth, caregiver sensitivity. Notably, the literature on caregiving-related adversity and associations between caregiving and brain development has focused on a wide array of caregiving-related behaviors (e.g., emotion socialization, assistance with emotion regulation, predictability of caregiving or home routines, caregiver warmth, etc.). The influence of specific caregiving-related behaviors is likely to be child- and context-specific such that it will be important for clinical assessment to involve delineation of the ways in which particular caregiving behaviors are associated with children's resilience in order to optimize intervention.

Building upon current efforts to chart sensitive periods of affective development and to identify patterns of experience-driven plasticity (L. Gabard-Durnam & McLaughlin, 2020; McLaughlin & Gabard-Durnam, 2022) is likely to enhance intervention approaches (Gee & Casey, 2015) and the potential to optimally support and repair stress-related alterations to neurobiological systems underlying emotion regulation (Sisk & Gee, 2022). Specifically, caregivers' role in buffering offspring neural and behavioral regulation changes from childhood to adolescence (Gee et al., 2014; Rogers et al., 2020) and therefore there are likely developmental stage-specific changes in the optimal role of caregivers in promoting resilience following adversity, which has important implications for developing targeted interventions. For example, consistent with the tasks of development specific to infancy and toddlerhood, evidence suggests that children who experienced adversity in the first five years of life may benefit from dyadic parent-child interventions focused on scaffolding opportunities to reaffirm caregivers' associations with safety and predictability, and to support children's emerging understanding of caregivers' capacity for repair (Gee & Cohodes, 2021; Lieberman et al., 2015). As another relevant example, accumulating evidence suggests that there may be opportunities during adolescence for reshaping of biological systems underlying the stress response for youth exposed to adversity early in life

in the context of a transition to enhanced caregiving quality (Colich et al., 2021; DePasquale et al., 2019, 2021; Gunnar et al., 2019). Despite the promise of these findings to inform the selection and timing of specific interventions, the role of pubertal recalibration in longer-term socioemotional functioning is not yet fully understood and recent longitudinal analyses suggest that recalibration may be associated with poorer adjustment in the longer term (N. B. Perry et al., 2020, 2022). The consideration of these developmental processes—alongside heterogeneity in individual- and family-level factors related to adversity—may inform when and for whom specific interventions have the potential to be maximally effective for shaping or reshaping caregiving influences on youth resilience (Cohodes, Kitt, et al., 2021; Gee et al., 2022; Ghosh Ippen et al., 2011; Sisk & Gee, 2022).

Finally, evidence suggests that supportive caregiving is a viable treatment target (Chu et al., 2021), and, further, that the neural mechanisms underlying caregiving influences on emotional development in the context of adversity can indeed be modified through psychotherapeutic intervention. As one example, a randomized controlled trial of a supportive parenting intervention for families living in poverty found that family participation in the Strong African American Families Program (SAAF) moderated the association between length of exposure to conditions of poverty and amygdala and hippocampal volumes among young adults. Specifically, whereas longer exposure to poverty during adolescence was associated with amygdala and hippocampal volume reduction among young adults whose families participated in the control condition (i.e., provision of informational brochures), this association was not detected among young adults whose families participated in SAAF (Brody et al., 2017). These findings suggest that supportive caregiving may buffer the risk of developing psychopathology in the context of adversity exposure (in this case, exposure to poverty), specifically via modulation of corticolimbic circuitry. Similarly, a recent study examined neurobiological changes associated with an early attachment intervention (Attachment and Biobehavioral Catch-Up; ABC; (Dozier & Bernard, 2019) for children exposed to caregiving-related adversity early in life. Children whose families engaged in ABC (relative to the control condition) showed greater activation of neural regions implicated in social cognition (e.g., hippocampus) to parental cues; further, the degree of parental cue-related activation was associated with more adaptive psychosocial functioning (Valadez et al., 2020). Taken together, these studies suggest that corticolimbic circuitry can be effectively modified in the context of psychosocial intervention focused on caregiving, and that targeted intervention has the potential to promote resilience following adversity by bolstering optimal caregiver influences on the developing brain and behavior. Building upon this promising line of work, delineating how psychosocial interventions may impact the neural bases of caregiver modulation of affective functioning across development will continue to shed light on ideal interventions for youth exposed to adversity. As one example, identifying evidence-based interventions that may facilitate the recovery of caregivers' capacity to provide optimal external regulation for youth following missed opportunities for provision of predictable, safe caregiver cues during early sensitive periods, or how dyadic or family-based interventions may exert distinct neurodevelopmental effects relative to individual treatments, will further inform efforts to optimize treatments for youth with adversity-related psychopathology (Gee & Cohodes, 2021).

Implications for policy

Developmental science has a notable history of influencing policy and fostering structural changes to better support youth and families. Findings from the Bucharest Early Intervention Project (Nelson et al., 2007) that demonstrated the consequences of parental deprivation and the importance of early intervention influenced societal shifts away from institutionalized care. Scientific knowledge of brain development and adolescent behavior has influenced numerous cases in the juvenile justice system (Casey et al., 2020; A. O. Cohen & Casey, 2014; Steinberg, 2017). Research on child development has been central to policymaking related to poverty reduction (Noble et al., 2021) and paid family leave (Brito et al., 2022).

Building directly on the research discussed here, theoretical and empirical advances in understanding the mechanisms by which caregivers promote resilience among youth exposed to adversity can inform public policy and public health-related efforts that prioritize the well-being of youth and families. Research reviewed thus far highlights the major impact of caregiving-related disruptions on child mental health due to the fact that, intrinsic to this experience, children are deprived of a primary mechanism of buffering and support. Relatedly, this empirical literature highlights the immense burden of repair when caregiving relationships are severed in contexts such as forced family separation, parental incarceration, or humanitarian crises like war or political violence. Here we outline specific recommendations for policymakers based on current understanding of the ways in which caregivers promote resilience following youth exposure to adversity.

First, the establishment and preservation of attachment relationships is essential to children's well-being and should be prioritized. Given the profound and lasting impact that caregiving-related adversity can have on developing brain and behavior—and the central role of caregivers in buffering children from the deleterious mental health impacts of exposure to adversity—policy should focus on supporting caregivers and preventing ruptures to children's attachment relationships. Second, while children can show remarkable capacity for resilience following adversity, policy must ensure that the burden of coping with adversity does not fall on individual youth and their families, particularly given disproportionate effects of adversity exposure and barriers to mental healthcare for families of lower-income and minoritized racial and ethnic backgrounds (R. E. Anderson et al., 2021; Condon et al., 2020; Shonkoff et al., 2021). Rather, changes should be enacted at the level of society and systems to maximally support children and their families. Indeed, consistent with the idea that resilience depends on multilevel interactions between multiple systems in society (Masten et al., 2021), evidence demonstrates that intervening at the family, community, or broader societal level is often most effective for promoting favorable outcomes following adversity (Feder et al., 2019; Gee, 2021b; Sapienza & Masten, 2011). Third, systems-level change should be enacted to eliminate systemic infliction of trauma on youth and families (Gee, 2022). While interventions can mitigate harm, addressing the broader societal forces that give rise to trauma is essential to prevention.

As an example of the policy-related implications of empirical research documenting the impacts of caregiving-related adversity, evidence of the consequences of caregiver-child separation and the essential role of caregivers in buffering children from the negative effects

of adversity (Cohodes, Kribakaran, et al., 2021; Sidamon-Eristoff et al., 2022) directly informed immigration policy related to the detention and forced separation of migrant families at the United States-Mexico border resulting from the United States government's "Zero Tolerance Policy" (Gee, 2021b; Gee & Cohodes, 2019), as well as the ruling that the U.S. government must provide access to mental health care for all separated families (Jordan, 2019). Despite reports of harm (Brabeck et al., 2014; Hampton et al., 2021; MacLean et al., 2019; Sidamon-Eristoff et al., 2022) and calls for structural changes to prevent the infliction of trauma against migrant children in the United States (Cohodes et al., 2020; Kribakaran & Gee, 2020; Pompa, 2019), migrant children and families continue to face separation, detention, exploitation, and deportation at alarming rates in the United States (Montoya-Galvez, 2022).

Developmental scientists have a unique and important role to play in informing broader discussions in society about adversity and youth well-being (Gee, 2022). Researchers can contribute to these ongoing discussions and policymaking by conducting rigorous science on childhood adversity, including on the central role of caregivers and families in promoting resilience, by sharing their findings in meaningful ways with broad audiences that go beyond the academic realm. In this work it is essential that our field works to center the voices of youth and families affected by adversity and embraces approaches to community-engaged research that directly involves affected youth and their caregivers throughout the research process (Collins et al., 2018; DePrince et al., 2022; Payán et al., 2022). Moreover, scholars in many other fields are conducting critical and complementary work; informing policy that prioritizes youth mental health will require interdisciplinary collaborations and partnerships.

Advances in this science, with the eventual goal of translating findings into clinical practice and informing policy, will require continuous refinement of conceptual models of early adversity to reflect the broader socioecological contexts in which children develop (Cicchetti & Lynch, 1993; Hyde et al., 2020; D. C. McCoy, 2013). Moreover, understanding resilience and trajectories of mental health in the context of early adversity necessitates consideration of distinct ways of experiencing and understanding these adversities (Biel & Coates, 2021; Danese & Widom, 2020; Pollak & Smith, 2021), as well as an emphasis on eradicating harmful societal forces such as structural racism that perpetually contribute to inequities in adversity exposure and mental health (Anglin et al., 2021; Bailey et al., 2017; G. C. Gee & Ford, 2011; Wildeman & Wang, 2017). Lastly, while adversity-related changes in neurobiology or behavior have often been framed as detrimental, such changes may be adaptive in the context of harsh or unpredictable environments (B. J. Ellis et al., 2017; Frankenhuis et al., 2020). Efforts to critically evaluate how we conceptualize adversity and effects on brain and behavioral development could both stimulate important scientific discoveries as well as shift the often dominant deficit-based narrative that can contribute to stigma of youth exposed to adversity (Gee, 2021a; Hanson & Nacewicz, 2021; Simmons et al., 2021). In conclusion, as developmental scientists, we have a collective responsibility to harness our knowledge of brain and behavioral development to improve the lives of youth—to affect systems-level change, to center the voices of youth, and, ultimately, to promote resilience among children and families.

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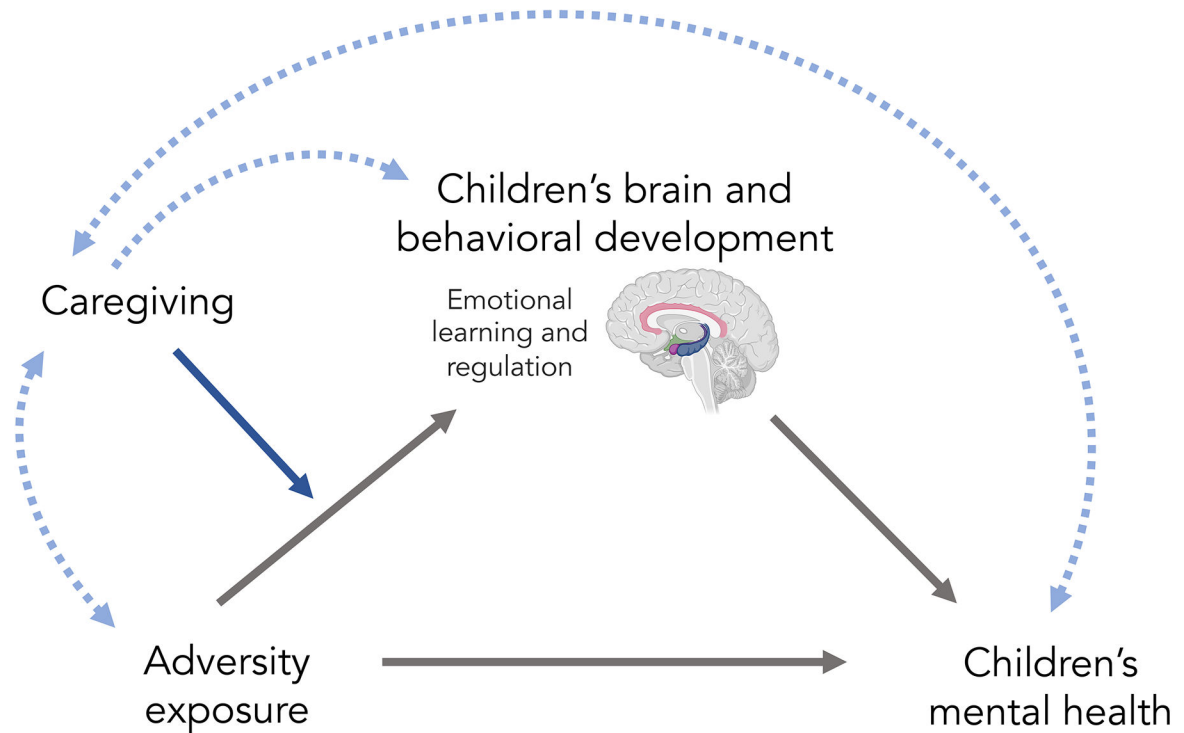


Figure 1. Conceptual model of how caregiving experiences can promote resilience in the context of adversity.

Exposure to adversity during development can increase risk for mental health disorders, with evidence suggesting that alterations in brain and behavioral development mediate this link. In particular, alterations in corticolimbic circuitry and processes related to emotional learning and regulation are important for understanding the effects of adversity on mental health. Caregiving experiences are a key factor that moderate the effects of adversity via relations with several constructs in this model. For example, caregivers can contribute to adverse experiences (e.g., via perpetration of maltreatment), affect brain and behavioral development, and directly influence children's mental health. Here we focus on the role that caregivers play in moderating the association between adversity and offspring brain and behavioral development. Caregivers can promote children's resilience by modulating the effects of adversity through their involvement in processes such as establishing safety and predictability and fostering emotion regulation. Brain image created with [BioRender.com](https://www.biorender.com).

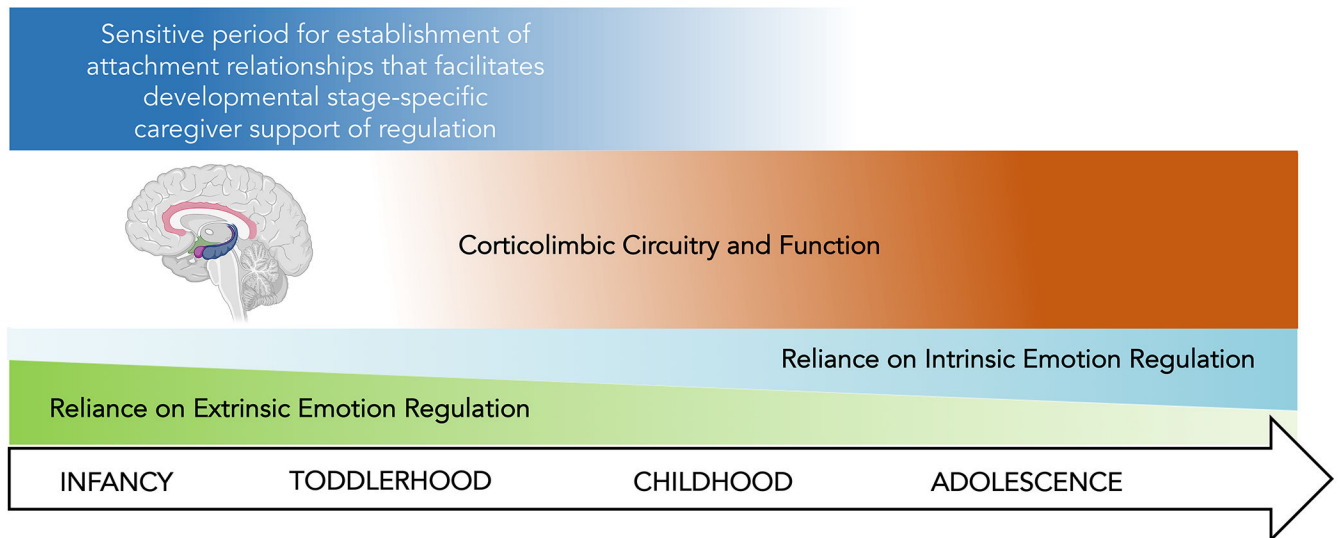


Figure 2. Caregiving influences and the development of corticolimbic circuitry that supports emotion regulation.

Cross-species evidence has identified a potential sensitive period, spanning infancy and toddlerhood, when caregiver inputs to the developing brain may have a particularly strong impact on the development of corticolimbic circuitry that supports emotion regulation. Specifically, caregiver inputs that are predictable and that are associated with safety may promote healthy neurodevelopment such that caregivers are able to support youth emotion regulation via modulation of this circuitry in later developmental stages. During infancy and toddlerhood, caregivers play a central role in regulating human amygdala function. As corticolimbic circuitry (e.g., connections between the medial prefrontal cortex and amygdala) matures (represented here by increasing intensity of the orange horizontal band), children experience a shift from greater reliance on extrinsic sources of emotion regulation to greater reliance on intrinsic emotion regulation (represented here by the increasing intensity of the blue band as the intensity of the green band decreases). Importantly, the optimal role of caregivers, the emotion regulation skills that youth are acquiring (and, perhaps, that caregivers are most likely to play a role in socializing), and the effects of adversity on these processes will all vary by developmental stage. Figure adapted with permission from Gee & Cohodes, 2021, *Current Directions in Psychological Science*. Brain image created with [BioRender.com](https://www.biorender.com).

Understanding the neurodevelopmental pathways linking early experiences and mental health

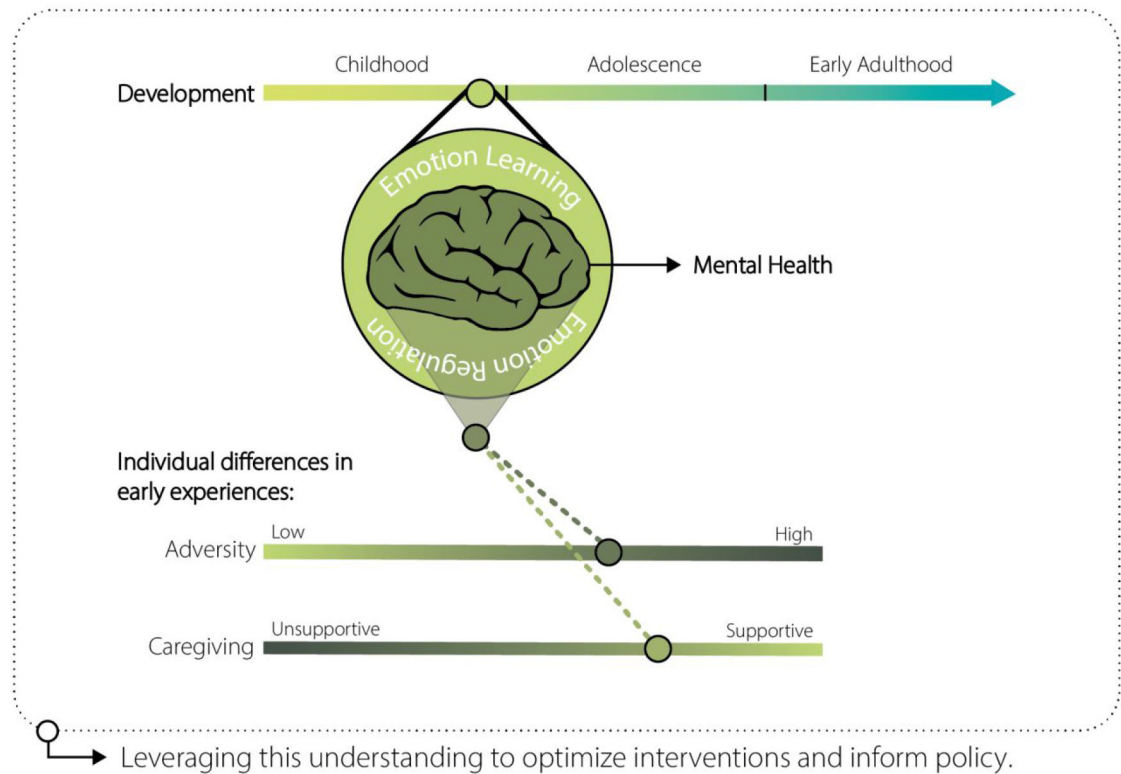


Figure 3. Applying knowledge of developmental stage and individual differences in early experiences to inform interventions and policy.

Experiences that occur early in life (e.g., adversity, caregiving) can have profound effects on development and mental health. Corticolimbic circuitry and related processes of emotion learning and regulation play a central role in linking early experiences with mental health. There is substantial heterogeneity in the nature and timing of early experiences and in neural and behavioral development. Developmental stage and individual differences in exposure to adversity and caregiving experiences relate to variability in neurodevelopmental pathways and mental health (here we represent variability in a given factor that differs across individuals via a spectrum of shading). Translating findings from this research can guide efforts to optimize interventions for youth with adversity-related psychopathology and to inform policy that supports the well-being of youth and families. Figure reproduced with permission from Gee, 2022, *American Psychologist*.