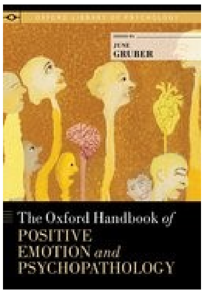

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CHAPTER

29 Protector and Casualty: The Dual Processes of Positive Emotion in Early-Life Adversity

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Abstract

Early-life adversity is associated with elevated risk for a wide range of mental disorders across the lifespan, including those that involve disruptions in positive emotionality. Although extensive research has evaluated heightened negative emotionality and threat processing as developmental mechanisms linking early-life adversity with mental health problems, emerging evidence suggests that positive emotions play an integral, but complex, role in the association of early-life adversity with psychopathology. This chapter identifies two pathways through which positive emotion influences risk for psychopathology following early-life adversity. First, experiences of early-life adversity may alter the development of the "positive valence system", which in turn increases risk for psychopathology. Second, the association between adversity and psychopathology may vary as a function of individual differences in positive emotionality. We consider how the development of positive emotionality—measured at psychological, behavioral and neurobiological levels—may be altered by early-life adversity, creating a diathesis for psychopathology. We additionally review evidence for the role of positive emotion, measured at multiple levels, as a protective factor that buffers against the adverse impacts of adversity. In integrating these two roles, it is proposed that characteristics of environmental adversity, including developmental timing, duration, and type of adversity, may differentially impact the development of positive emotionality, leading to a better understanding of risks associated with specific adverse experiences. Methodological issues regarding the measurement of adverse environments as well as implications for early intervention and treatment are discussed.

Keywords: early life adversity, protector, casualty, positive emotionality, adverse environments, mental health problems

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Introduction

Early-life adversity represents one of the most potent risk factors for psychopathology across the life span (Green et al., 2010; McLaughlin et al., 2012), including disorders that involve disruptions in emotionality. Early-life adversity is common: Population studies estimated that approximately one third to one half of children have experienced at least one such experience, in both the United Sates and cross nationally (Green et al., 2010; Kessler et al., 2010), highlighting the importance of identifying the influence of these experiences on psychological and neurobiological development. Although extensive research has linked heightened negative emotionality and threat processing with early-life adversity, emerging evidence suggests that early-life adversity is also linked with disruptions in positive emotionality. Disorders commonly associated with early-life adversity, such as post-traumatic stress disorder (PTSD), depression, and substance use, are often characterized by disruptions in positive emotionality (Dube et al., 2003; Green et al., 2010; McLaughlin et al., 2012; Widom, 1999; Widom, DuMont, & Czaja, 2007). Early-life adversity not only is associated with elevated risk for onset of these disorders, but also predicts earlier age of onset (Wilson, Vaidyanathan, ↳ p. 497 Miller, McGue, & Iacono, 2014); greater symptom complexity (Cloitre et al., 2009) and severity (Lumley & Harkness, 2007; McLaughlin et al., 2010); high rates of comorbidity and disability (Widom et al., 2007); and poor response to evidence-based treatments for depression (Nanni, Uher, & Danese, 2012). Studies directly examining the moderating effect of early-life adversity on treatment response to evidence-based treatments for PTSD and substance use are needed (Cloitre, 2015). Furthermore, specialist treatments in this population may be needed (Cloitre, 2015; Sullivan & Cadcii, 1994; Teicher & Samson, 2013).

In this chapter, we examine multiple pathways through which positive emotion may contribute to development of psychopathology following early-life adversity. On one hand, early-life adversity may disrupt the development of systems underpinning positive emotion, contributing to heightened risk for psychiatric disorders. We first review evidence for this pathway by exploring the association of diverse forms of early-life adversity with disturbances in positive emotionality and the neurobiological systems that support these emotions. We consider how the development of positive emotionality—measured at psychological, behavioral, and neurobiological levels—may be altered by early-life adversity, creating a diathesis for psychopathology. Extensive evidence suggests that disruptions in positive emotionality and reward processing are a transdiagnostic factor involved in multiple forms of psychopathology; this literature is reviewed by David Watson and Kasey Stanton in Chapter 6 this volume and is not repeated here. On the other hand, not all children who experience adversity go on to experience mental health problems. A small, but growing, literature suggests that higher levels of positive emotion and sensitivity to rewards may increase resilience to certain mental health problems following exposure to early-life adversity.

We additionally review evidence for the role of positive emotion, measured at multiple levels, as a buffer against the harmful impact of early-life adversity. As such, we propose that positive emotion is a cause of mental health problems following early-life adversity, as well as a protector against negative mental health outcomes associated with adversity. In integrating these two roles of positive emotion—as both a mediator and a moderator—we propose that characteristics of environmental adversity, including developmental timing, duration, and type of adversity, may differentially impact the development of positive emotionality, and that study of the differential effects of such characteristics will lead to a better understanding of risks associated with specific adverse experiences. We then discuss methodological issues regarding the measurement of adverse environments, as well as implications for early intervention and treatment. Identifying how these processes unfold across development is critical for understanding the conditions that lead to both risk for and resilience to mental health problems following early-life adversity, with the potential to inform how, when, and with whom to intervene.

Key Terms and Methods

Early-Life Adversity: Dimensions of Deprivation and Threat

McLaughlin (2016) recently defined early-life adversity as an environmental event or series of events during childhood that are severe or continue over time and that “are likely to require significant adaptation by an average child and that represent a deviation from the expectable environment” (p. 4). These include experiences that result in the absence of expected inputs (i.e., caregiver neglect, environmental deprivation, poverty, institutionalization) or the presence of unexpected inputs that represent significant threats to physical integrity or well-being of the child (i.e., exposure to violence, and physical, sexual or emotional abuse) (McLaughlin, 2016).

We review literature linking early-life adversity and positive emotion in light of a recent conceptual model of adversity that distinguishes between the dimensions of threat and deprivation (McLaughlin, 2016; McLaughlin, Sheridan, & Lambert, 2014; Sheridan & McLaughlin, 2014). Experiences of threat involve harm or threat of harm, such as exposure to abuse or other forms of interpersonal violence, whereas deprivation involves an absence of expected social, emotional, and cognitive inputs from the environment, as in neglect, institutional rearing, and poverty (McLaughlin, 2016; Sheridan & McLaughlin, 2014). Although many studies have historically examined experiences of threat and deprivation as indicators of the same underlying construct (i.e., maltreatment), some studies have systematically compared associations of specific adversity types with positive emotionality (Pollak, Cicchetti, Hornung, & Reed, 2000; Young & Widom, 2014). We hypothesize that the development of positive emotion processing varies in response to these different early environmental contexts. Specifically, on the one hand, deprivation is likely to be associated with a lack of learning about the significance of positive emotional cues due to the lack of contingent parental responding and absence of positive social and emotional inputs early in development, which may present as global deficits across positive emotion domains. On the other hand, threatening environments may not entirely lack positive emotional cues, although they are likely overshadowed by the presence of emotional cues predicting danger, which may result in variable responses to positive emotion across domains.

Positive Emotionality and the Dopamine System

For the purpose of this review, we have considered positive emotion to encompass the “Positive Valence System,” a broad domain described as the set of systems that underlies engagement in positive environmental situations and contexts that include five expert consensus constructs (PVS Workgroup, 2011). Consistent with Olino (2016), we focus on only four of these constructs: approach motivation, initial responsiveness to reward attainment, sustained responsiveness to reward attainment, and reward learning (Table 29.1) (we exclude habit). Together, this model provides a conceptually coherent set of processes involved in identifying rewards, engaging in behaviors that lead to obtaining rewards, and experiencing satisfaction from rewards (Olino, 2016). One of the guiding principles of this conceptual approach is that unique information about the Positive Valence System can be derived from multiple levels of analysis, including analysis of genes, neural circuitry, and behavior among others (PVS Workgroup, 2011).

Table 29.1. Domain constructs within the Positive Valence System

	Approach Motivation "Wanting"	Initial Responsiveness to Reward Attainment "Liking"	Sustained Responsiveness to Reward Attainment	Reward Learning
Description and specific processes involved in each construct	The regulation of behaviors that result in reward achievement, including the following processes: • Reward valuation • Willingness to work (given costs to achieve a reinforcer) • Expectancy of reward • Preference-based decision- making	Initial reactions of liking or enjoying rewards; the culmination of reward seeking: • Hedonic responses during consummation of rewards	Processes involved in the termination of reward seeking: • Cues of completion of reward pursuit • Satiety of rewards	Processes that determine the strength of associative learning based on positive reinforcement: • Linking information about stimuli and contexts with positive outcomes

Note: Adapted from the PVS Work Group (2011).

At the neurobiological level, the neurotransmitter dopamine within the mesolimbic and mesocortical systems plays a key role in multiple Positive Valence System constructs. The mesolimbic pathway refers to dopaminergic projections from the midbrain (ventral tegmental area) to the striatum, and the mesocortical pathway refers to projections from the striatum to the prefrontal cortex (PFC). The mesolimbic pathway, including the ventral (i.e., nucleus accumbens) and dorsal striatum, is involved in most, if not all, Positive Valence System processes (Haber & Knutson, 2010; Nestler & Carlezon, 2006). Within the mesocortical pathway, several regions in the PFC are central: The orbitofrontal cortex (OFC) is involved in reward evaluation, the dorsal anterior cingulate cortex (ACC) is involved in evaluating the effort necessary to gain a reward, and the ventromedial (vmPFC) and dorsolateral prefrontal cortex (dlPFC) are involved in making decisions concerning effort and value assessments (Der-Avakian & Markou, 2012; Kringelbach, 2005; Montague, King-Casas, & Cohen, 2006; Rudebeck, Saunders, Prescott, Chau, & Murray, 2013). Dopamine-related function can be examined directly in animal models (Der-Avakian & Markou, 2012; Russo & Nestler, 2013), whereas most human studies of the Positive Valence System examine structural and functional properties of dopamine-related brain networks via both functional and structural magnetic resonance imaging (fMRI/MRI). Another measure of brain function used to examine reward processing is electroencephalogram (EEG), which detects electrical activity in the brain with higher temporal resolution, but poorer spatial resolution, than fMRI. In this review, we consider studies that describe differences in dopamine-related processes and circuitry associated with early-life adversity as evidence of adversity-related disruptions to positive emotion.

The Positive Valence System also incorporates psychological and behavioral phenomena as indices ↳ of the domain constructs. There are many self-report measures of positive emotion that tap various constructs within the Positive Valence System, although the measurement of positive emotion within the early-life adversity literature has primarily focused on behavioral measures, which are often correlated with neurobiological properties (for an excellent summary of psychological and behavioral measures of positive emotion, see Olino, 2016). Behavioral tasks designed to measure Positive Valence System functioning primarily assess approach motivation and reward learning (Olino, 2016). Adaptations of behavioral tasks for fMRI, such as the monetary incentive delay task (Knutson, Westdorp, Kaiser, & Hommer, 2000), have been used to explore neural responses associated with initial and sustained responsiveness to reward. Similarly, passive viewing of affective stimuli during fMRI has also been used to assess initial responsiveness to reward (Dennison et al., 2016; Goff et al., 2013). We provide a more detailed overview of both animal and human paradigms.

Animal Models of Early-Life Adversity

Early-life adversity is typically modeled in animals by separating infant offspring from their mothers. In rodents, early maternal separation involves separating infant pups from mothers on a variable schedule for up to 4 hours per day, while keeping the litter intact (Rüedi-Bettschen, Pedersen, Feldon, & Pryce, 2005). Other variations involve either separating pups from their mothers pre- or postweaning or placing pups with a foster mother (for a description of the maternal variation paradigm, see D'Amato et al., 2011; Plotsky & Meaney, 1993). Early deprivation is a more severe form of maternal separation, involving separating individual pups from both dams and siblings (Rüedi-Bettschen et al., 2005). The effects of early maternal separation and deprivation have also been studied under different environmental conditions involving manipulation of housing conditions, such as temperature and light schedules (Rüedi-Bettschen et al., 2005). A similar protocol for maternal separation has been used in primates (Dettling, Feldon, & Pryce, 2002; Suomi, Collins, Harlow, & Ruppenthal, 1976), although in some maternal separation paradigms twin offspring are consecutively removed from the mother and placed in isolation such that the mother is never separated from both infants at the same time (Dettling et al., 2002). Observational studies have examined naturally occurring variation in postnatal maternal behavior (e.g., licking/grooming) as indicators of adversity, which have been linked to differences in stress reactivity and exploratory behavior (Caldji et al., 1998; Francis, Champagne, Liu, & Meaney, 1999; Liu et al., 1997). Finally, artificial rearing—the most severe form of maternal and environmental deprivation—involves removing animals prior to weaning, surgically eliminating oral feeding, and placing them in isolation for an extended period of time (Hall, 1975; Lomanowska, Rana, McCutcheon, Parker, & Wainwright, 2006).

Measurement of Positive Emotionality in Animal Models

Alterations to appetitive behavior following early maternal separation or deprivation have been measured in numerous ways (Matthews & Robbins, 2003). Gustatory and social preference tests for primary reinforcers have assessed basic consumption behavior thought to be associated with approach motivation (Berridge, Robinson, & Aldridge, 2009). Reduced preference for a primary reinforcer is thought to signal anhedonia (Willner, Muscat, & Papp, 1992). An extension of this preference test is the incentive contrast sensitivity test. This test measures the degree to which changes in the magnitude of rewards alter behavior; these changes are thought to signal emotional responses in rodents (Matthews & Robbins, 2003) and indicate sustained responsiveness to rewards. Locomotor responses to novel environments, an appetitive stimulus for rodents indicative of initial responsiveness to rewards, have also been used to assess differences in appetitive behavior (Matthews & Robbins, 2003). Preferences for conditioned incentives (i.e., Pavlovian conditioning) have been assessed by recording locomotor activity in environments paired with food rewards, as well as time spent in places paired with food rewards. Operant methods assessing appetitive behaviors involve observing how hard animals will work for rewards (i.e., food, drug, and social) under fixed and progressive ratio schedules of reinforcement by measuring number of bar presses, number of reinforcements obtained, and final ratio attained before breaking point (Rüedi-Bettschen et al., 2005; Shalev & Kafkafi, 2002). Tests of behavior under both Pavlovian and operant conditioning are thought to measure reward learning (PVS Workgroup, 2011).

Finally, intracranial self-stimulation, whereby electrodes stimulate key nodes within the neural reward system (Markou & Koob, 1992), has been used to evaluate differences in central reinforcement processes resulting from maternal separation (Matthews & Robbins, 2003). In this paradigm, ↳ researchers determine a threshold for electrical stimulation as the point where the animal is willing to perform a behavior (i.e., run in a wheel) for electrical stimulation, which acts as a positive reinforcer. Variations in this threshold as a function of drug or stress exposure are then compared between groups differentially exposed to early-life adversity. Decreases in these thresholds are interpreted as reward-enhancing effects, whereas elevations in thresholds indicate anhedonia. Alterations in brain stimulation behavior resulting from early maternal separation are taken as evidence that adversity affects primary motivational processes.

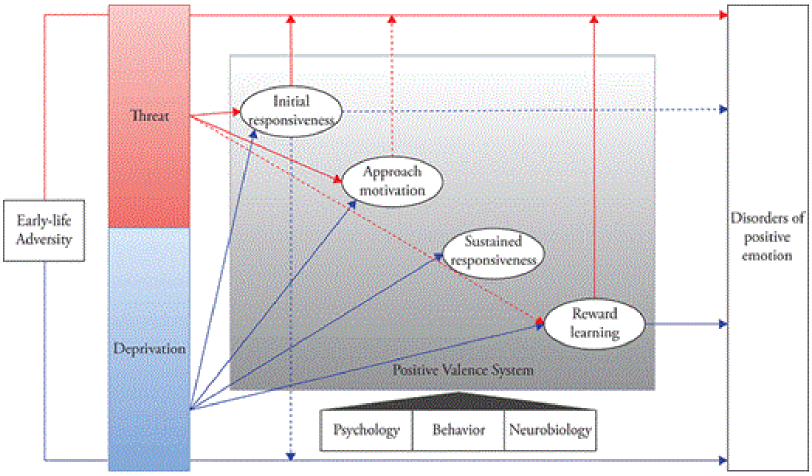
Measurement of Positive Emotion in Humans

The most commonly used tasks examining positive emotion in human children measure emotional responses to positive stimuli or ask participants to identify emotion in faces, often while tracking central neurobiological responses (i.e., event-related potentials [ERPs] from electroencephalogram studies or blood oxygen level–dependent [BOLD] response in fMRI). Neurobiological responses while viewing positive stimuli provide indices of initial responsiveness to reward. Other studies have used incentive-based tasks that pair neutral stimuli with rewards, such as the monetary incentive delay task (Knutson et al., 2000), guessing or gambling games (Guyer et al., 2006), or incentive-based decision-making tasks (Pechtel & Pizzagalli, 2013). These studies typically measure both behavior (i.e., accuracy, reaction rime) and central neurobiological responses as indicators of positive emotion processes. Neurobiological responses on these tasks can sometimes be mapped onto discrete subcomponents of Positive Valence System functioning; for example, brain activation during anticipation of reward indexes approach motivation, whereas activation on receipt of reward signals initial responsiveness to reward. Behavioral measures on these tasks provide less precise measurement of Positive Valence System components, arguably incorporating multiple Positive Valence System domains (e.g., reaction time and accuracy differences based on reward value in a monetary-incentive delay task reflect both approach motivation and reward learning). Anatomical differences (i.e., structural MRI) in dopamine-related circuits associated with early-life adversity may indicate stable and enduring disruptions to positive emotion processing. Several studies have also examined trait positive affect or temperament as an outcome measure following early-life adversity (Dillon et al., 2009; Ghera et al., 2009; Goff et al., 2013; Smyke et al., 2007).

Casualty: Adversity-Related Disruptions to Positive Emotion

Evidence from both animal and human studies suggests that childhood experiences of adversity are associated with lasting changes in positive emotion, measured at behavioral and physiological levels. We first review evidence from animal studies, followed by evidence from human studies. A summary of the findings from both the animal and human literature is depicted in Figure 29.1. Figure 29.1 summarizes main effects of early-life adversity on Positive Valence System domains and evidence supporting the role of this system as a moderator of the association between early-life adversity and disorders of positive emotion.

Figure 29.1



Current evidence from both human and animal studies of main effects of adversity on Positive Valence System (PVS) domains and evidence supporting the role of PVS domains as moderators and mediators of the relationships between early-life adversity and disorders of positive emotion. Main effects of PVS on disorders of positive emotion are not depicted. Blue lines = deprivation pathway; red lines = threat pathway; solid lines = evidence for an association; dotted lines = mixed evidence or tested in maltreatment sample (i.e., both threat and deprivation exposure). Note: Animal studies of maternal separation are conceptualized here as deprivation-related exposures, although it has been proposed that these animal models could involve exposure to both threat and deprivation (see McLaughlin, Sheridan, & Lambert, 2014).

Animal Studies

Behavioral Effects of Early-Life Adversity

Animal studies of early maternal separation and deprivation have documented alterations in a wide range of the appetitive behaviors described previously toward a variety of reward types (i.e., food, drug, and social rewards), which are apparent in adolescence and endure into adulthood. However, specific findings are mixed, with studies reporting no effects of adversity (Shalev & Kafkafi, 2002); decreases in appetitive behaviors (Leventopoulos, Russig, Feldon, Pryce, & Opacka-Juffry, 2009; Martini & Valverde, 2012; Matthews & Robbins, 2003; Michaels & Holtzman, 2007; Mintz, Rüedi-Bettschen, Feldon, & Pryce, 2005; Paul, English, & Halaris, 2000; Pryce, Dettling, Spengler, Schnell, & Feldon, 2004; Rüedi-Bettschen et al., 2005, 2006; Sasagawa et al., 2017; Ventura et al., 2013); and increases in appetitive behaviors (Higley, Hasert, Suomi, & Linnoila, 1991; Lomanowska et al., 2006; Michaels & Holtzman, 2006; E. E. Nelson et al., 2009). Differences in timing of maternal separation, severity of environmental deprivation or adversity, and variations in the measurement of appetitive behavior may contribute to variability in the findings, although we are unaware of any meta-analyses clarifying these issues (for a review of experimental issues, see Pryce & Feldon, 2003). These findings are summarized in Table 29.2, which (a) maps behavioral measures onto Positive Valence System domains and (b) identifies variables that may be associated with contrary findings. Both rodent and nonhuman primate studies are included.

Table 29.2. Summary of findings of effects of early maternal separation and deprivation on development and appetitive behaviors observed in adolescence and adulthood

Behavior	Proposed PVS Domain(s)	Enhanced	Attenuated	No Effect
Weight gain	Sustained responsiveness	Morgan & Einon, 1975[a] Matthews, Hall, et al., 1996 Matthews, Wilkinson, et al. 1996		
Food consumption	Initial responsiveness Sustained responsiveness	Morgan & Einon, 1975[a]		Sasagawa et al., 2017
Locomotor response to novelty	Initial responsiveness	Jones, Marsden, & Robbins, 1990[a] Phillips, Howes, Whitelaw, Wilkinson, et al., 1994[a] Lomanowska et al., 2006[b]	Matthews, Wilkinson, et al., 1996	
Sucrose/saccharin/food preference	Approach motivation	Michaels & Holtzman, 2006[c] Lomanowska et al., 2006[b] Nelson et al., 2009[b,e] Brenes & Fornaguera, 2008[a]	Paul et al., 2000 Rüedi-Bettschen et al., 2006[d] Ventura et al., 2013[c]	Matthews, Hall, et al., 1996 Matthews, Wilkinson, et al., 1996 Shalev & Kafkafi, 2002 Jones et al., 1990[a]
Preference for social environments	Approach motivation		Mintz et al., 2005[b] Rüedi-Bettschen et al., 2006	
Preference for alcohol	Approach motivation	Higley et al., 1991 García-Gutiérrez et al., 2016		
Incentive contrast sensitivity	Sustained responsiveness		Matthews, Wilkinson, et al., 1996	

Pavlovian appetitive conditioning	Reward learning	Jones, Marsden, & Robbins, 1990[a] Lomanowska et al., 2006[b]	Matthews, Hall, et al., 1996 Matthews, Wilkinson, et al., 1996[d] Ventura et al., 2013[c] Sasagawa et al., 2017[d]	Faure, Stein, & Daniels, 2009
Operant appetitive conditioning	Reward learning	Jones et al., 1990[a]	Phillips, Howes, Whitelaw, Robbins, et al., 1994[a] Phillips, Howes, Whitelaw, Wilkinson, et al., 1994[a] Leventopoulos et al., 2009 Rüedi-Bettschen et al., 2006[d] Rüedi-Bettschen et al., 2005[b] Pryce et al., 2004[e] Martini & Valverde, 2012[e]	Shalev & Kafkafi, 2002
Behavioral sensitivity to dopamine D_2 receptor antagonist	? Approach motivation ? Initial responsiveness ? Sustained reponsiveness	Matthews, Hall, et al., 1996 (low dose) Matthews & Robbins, 2003	Phillips, Howes, Whitelaw, Robbins, et al., 1994a[a]	Matthews, Robbins, Everitt, & Caine, 1999
Behavioral sensitivity to dopamine D_1 receptor antagonist	? Approach motivation ? Initial responsiveness ? Sustained reponsiveness		Phillips, Howes, Whitelaw, Robbins, et al., 1994a[a] (low dose)	Matthews, Hall, et al., 1996 Matthews et al., 1999
Locomotor response to noncontingent systemic cocaine/d-amphetamine	Initial responsiveness	Jones et al., 1990[a] (low dose) Phillips, Howes, Whitelaw, Wilkinson, et al., 1994[a] Meaney et al., 2002	Matthews, Hall, et al., 1996[d] (low dose)	
Cocaine/d-amphetamine self-administration (high dose)	Approach motivation	Matthews et al., 1999[d]	Phillips, Howes, Whitelaw, Robbins, et al., 1994[a]	

Cocaine/d-amphetamine self-administration (low dose)	Approach motivation		Matthews et al., 1999[d]	Howes, Wilkinson, Robbins, & Everitt, 1995[a] Phillips, Howes, Whitelaw, Robbins, et al. 1994[a]

a Post weaning maternal separation

b Effects observed under conditions involving additional environmental adversity (i.e., exposure to darkness and/or cold, artificial rearing, permanent rather than intermittent maternal separation)

c Pups were exposed to maternal variation (i.e., fostered) not separation

d Evidence of sex differences

e Measurement during in adolescence not adulthood.

PVS = Positive Valence System.

p. 501 Studies of intracranial self-stimulation have shown no differences in baseline threshold levels between control animals and those exposed to maternal separation (Der-Avakian & Markou, 2010; Matthews & Robbins, 2003). Maternal separation has been associated with blunted threshold response to heroin (Matthews & Robbins, 2003), but findings with d-amphetamine were mixed, with one study reporting no effects of rearing condition (Matthews & Robbins, 2003) and another reporting that maternally separated rats exhibited lower thresholds compared with controls (Der-Avakian & Markou, 2010), indicating increased sensitivity to the rewarding properties of this drug. The discrepancy may be a function of differences in the timing of maternal separation across studies (Postnatal Day 1 for Der-Avakian & Markou, 2010, versus Day 5 for Matthews & Robbins, 2003). Given that natural variations in maternal care are most pronounced during the first week (Champagne, Francis, Mar, & Meaney, 2003), it is possible that disruption of the dams and pups during this initial postnatal period influenced developmental outcomes in different ways to later separation, a possibility that requires further investigation.

Findings reported in Table 29.2 suggest that maternal separation affects a number of components within the Positive Valence System, including initial and sustained responsiveness, approach motivation, and reward learning. However, in each of these domains contrary findings of enhanced and attenuated effects, or no effects, on behavior have been observed, highlighting the need for further studies and meta-analysis to clarify these associations. One explanation for these contrary findings is that heightened response to reward may not represent any functional alteration in reward circuitry but may instead be a behavioral palliative for the negative emotions and arousal experienced to a greater degree in animals exposed to maternal separation. Indeed, studies that have reported *enhanced* reward response following early adversity have also reported concurrent heightened response to aversive stimuli, suggesting global hyperemotionality following early adversity (Nelson et al., 2009). In explaining their finding that maternally deprived rhesus monkeys showed decreased preference for sucrose, but consumed more quinine-flavored water than controls, Paul and colleagues (2000) suggested that “anhedonia” in animal
p. 502 models may be secondary to ↳

p. 503 ↳

p. 504 ↳

a generally attenuated responsiveness to stimuli, rather than a unitary reduction in responsiveness to the appetitive properties of stimuli.

However, as we review in material that follows, numerous studies suggested direct effects of adversity on brain systems that respond to rewarding stimuli. A recent study reported associations between early maternal separation and both depression-like behavior and increased vulnerability to ethanol consumption during adolescence. Such behavior was exacerbated by exposure to novel stressful stimuli in adolescence (García-Gutiérrez et al., 2016), suggesting that early maternal separation may create shared vulnerability for both anhedonia and substance use disorders, but the mechanism linking or differentiating these two responses remains unclear (Volkow, 2004).

Differential effects of early-life adversity on different components of the Positive Valence System may also help explain discrepant findings, although few studies have systematically tested effects on different aspects of the Positive Valence System (see Table 29.1 for definitions of the subcomponents of the Positive Valence System), for example, one type of adversity may affect approach motivation but leave initial responsiveness unaffected. We are aware of at least one study that has considered unique processes of approach motivation (i.e., wanting) and reward responsiveness (i.e., liking). In adolescent monkeys, Pryce and colleagues (2004) showed that early deprivation-dependent reductions in appetitive operant behavior were not accompanied by deficits in consummatory behavior, suggesting that early deprivation deficits may be specific to approach motivation (wanting) and reward learning, rather than consummatory behavior (liking). Yet, as highlighted previously, a number of studies in other laboratories have reported enhanced appetitive consumption behavior resulting from early-life adversity. Interestingly, the findings for increased consummatory behavior are derived from studies that deviated from early maternal separation or early deprivation paradigms and involved exposure to more severe adversity (Lomanowska et al., 2006; Nelson et al., 2009), social isolation after weaning (Brenes & Fornaguera, 2008), and maternal disruption rather than separation (Michaels & Holtzman, 2006). More precise descriptions of which appetitive system is affected by early adversity and how it is affected are needed to clarify the core mechanisms linking early adversity to alterations in positive emotion.

While, on balance, there is considerable evidence that early maternal separation results in disturbances in appetitive behavior, variable findings in the effects of early maternal separation and early deprivation outlined in Table 29.2 suggest imprecise characterization of the specific conditions that culminate in enduring disturbance to appetitive behavior, including sex, environmental characteristics, and developmental timing of both exposure and testing. Indeed, studies have reported differences in the effects of early maternal separation on appetitive behavior as a function of sex (Matthews, Wilkinson, & Robbins, 1996) and stress-inducing housing conditions during separation (Rüedi-Bettschen et al., 2005). Surprisingly, examination of sensitive periods associated with the greatest negative impact of early maternal separation on appetitive behavior is limited, although some evidence suggests that earlier exposure to adversity resulted in greater disruptions in behavioral indicators of positive emotion. For example, in rats, maternal separation after weaning was associated with greater locomotor activity in novel environments (Phillips, Howes, Whitelaw, Wilkinson, et al., 1994), whereas separation prior to weaning was associated with attenuated locomotor response to novelty (Matthews, Wilkinson, et al., 1996). There are several cases where timing of separation appeared to result in contrary effects: Rats separated postweaning exhibited reduced response to the effects of dopamine D_1 and D_2 antagonists on cocaine self-administration (Phillips, Howes, Whitelaw, Robbins, & Everitt, 1994), whereas rats separated prior to weaning exhibited increased sensitivity to the effects of D_2 antagonist on conditioned locomotor activity (Matthews, Hall, Wilkinson, & Robbins, 1996).

In a systematic study of developmental effects, Roque, Mesquita, Palha, Sousa, and Correia-Neves (2014) found that earlier but not later maternal separation (i.e., separation on Days 2–15 vs. Days 7–20) in rats was associated with depressive-like behaviors in adulthood. Although their assessment of depression using the forced swim test did not assess appetitive behavior as described previously, this test is highly correlated with appetitive behavior (Bessa et al., 2009). Thus, timing of adversity may be associated with differential effects on positive emotion functioning, consistent with evidence that programming of dopaminergic circuits is both dynamic in early development and sensitive to endocrine stress responses, including high levels of ↳ glucocorticoids (Rodrigues, Leão, Carvalho, Almeida, & Sousa, 2011).

Early adversity also appears to alter appetitive responses to subsequent stressors. In adulthood, maternally separated rats exhibited greater sensitization to amphetamine than handled or never-handled rats following repeated stress-inducing saline injections (Meaney, Brake, & Gratton, 2002). Exposure to additional new stressful stimuli (i.e., wet cages, urine from other species, restraint stress) significantly increased vulnerability to ethanol consumption induced by maternal separation in mice (García-Gutiérrez et al., 2016). Early maternal separation led to reductions in motivated behavior in response to escapable shock during adolescence, which also varied by sex (Leussis, Freund, Brenhouse, Thompson, & Andersen, 2012). In adulthood, acute social defeat—a paradigm that exposes rats to physical defeat from another socially dominant animal—initially produced anhedonia in control rats, but not in maternally separated rats (Der-Avakian & Markou, 2010). However, while control rats habituated to prolonged social defeat stress, maternally separated rats exhibited an increased anhedonic response to the repeated stressor (Der-Avakian & Markou, 2010). Interestingly, 1 week after social defeat stress exposure ended, maternally separated rats still exhibited an increased reward-enhancing effect of acute amphetamine administration compared with controls (Der-Avakian & Markou, 2010). Thus, early-life adversity may increase an individual's vulnerability to depressive or addictive disorders when confronted with stress or drug exposure later in life (Der-Avakian & Markou, 2010).

In sum, the current evidence suggests that early adversity is associated with alterations to appetitive behavior across all subcomponents of the Positive Valence System. Yet, clarification of the specific effects of early adversity requires further consideration of the effects of individual differences such as sex, environmental characteristics, and developmental timing of exposure to adversity.

Neurobiological Effects of Stress and Early-Life Adversity

Numerous animal studies have shown that both acute mild and sustained uncontrollable stressors resulted in changes in dopaminergic activity in the striatum and PFC. The effects of stress exposure on dopamine release in two key brain pathways associated with positive emotion, the mesolimbic and mesocortical systems, appeared not only to differ from one another, but also to differ as a function of the type of stressor (controllable/uncontrollable) and the duration of the stressor (acute/chronic) (Pizzagalli, 2014). Further, prior exposure to chronic stress altered dopamine response to subsequent acute stressors (Pizzagalli, 2014). A large literature has examined the effects of chronic and prolonged stress exposure on the mesolimbic and mesocortical reward systems (for a review of the neurobiological effects of stress on reward neurocircuitry, see both Cabib & Puglisi-Allegra, 2012; Pizzagalli, 2014). We briefly review this literature before turning to the smaller body of literature specifically examining early-life adversity.

While dopamine release in the nucleus accumbens increased when exposed to a short, novel, or controllable stressor (Chrapusta, Wyatt, & Masserano, 1997), prolonged exposure to uncontrollable or inescapable stressors led to inhibition of dopamine activity in the mesolimbic pathway (Imperato, Angelucci, Casolini, Zocchi, & Puglisi-Allegra, 1992; Pizzagalli, 2014; Rossetti, Lai, Hmaidan, & Gessa, 1993). For example, acute restraint stress in animals resulted in extracellular dopamine in the nucleus accumbens for the first 3 days of testing but not on a subsequent fourth day (Imperato et al., 1992), and exposure to chronic inescapable stressors produced a dramatic reduction in the number of spontaneously active dopamine neurons in the ventral tegmental area (Moore, Rose, & Grace, 2001). Changes in mesolimbic dopamine regulation arising from chronic stress also appeared to be long lasting (Cabib & Puglisi-Allegra, 2012). For example, after a 3-week exposure to unavoidable stress, rats showed reductions in dopamine output in the nucleus accumbens 14 days after the last stress administration (Mangiavacchi et al., 2001). Additionally, reduced dopamine transmission in the mesolimbic pathway has been observed in the ventral and dorsal striatum of adult animals exposed to a variety of chronic stressors, including prolonged early maternal separation (Brake, Zhang, Diorio, Meaney, & Gratton, 2004); prolonged immobilization (Lucas, Wang, McCall, & McEwen, 2007); and psychosocial stress (i.e., exposure to subordination in social dominance hierarchies) (Isovich, Mijnster, Flugge, & Fuchs, 2000; Lucas et al., 2004).

Early maternal separation is associated with multiple alterations in the mesolimbic dopamine system in adulthood. Maternal separation during the first 14 days of life resulted in lower density of the nucleus accumbens and striatal dopamine transporter sites at 3 months of age (Brake et al., 2004), and early deprivation-dependent reductions ↳ in D_2 binding in the dorsolateral striatum and nucleus accumbens were observed among adult rats (Leventopoulos et al., 2009). Maternal separation was associated with reductions in adult dopamine transporter binding levels in the striatum: Dopamine transporter levels in the nucleus accumbens and dorsal striatum were up to 250 percent greater in controls compared to maternally separated rats, with no group differences in the frontal cortex and ventral tegmental area (Meaney et al., 2002). Early maternal separation was also associated with increased gene expression in the mu-opioid and tyrosine hydroxylase receptors in the ventral tegmental area and nucleus accumbens during adolescence (García-Gutiérrez et al., 2016); mu-opioid receptors play a major role in substance reinforcement and dependence (Mendez & Morales-Mulia, 2008). Further, early maternal separation was also associated with alterations in endogenous opioids within several regions of the mesolimbic reward system; the nature of these effects, however, were complex, varying by separation condition (individual or litter) and duration of separation (Gustafsson, Oreland, Hoffmann, & Nylander, 2008; Nylander & Roman, 2012). For example, compared to controls, individually separated rats had higher basal opioid peptide levels in the nucleus accumbens, whereas litter-separated rats did not show these differences (Gustafsson et al., 2008). Interestingly, both duration and conditions of separation affected opioid peptide levels across maturation (Gustafsson et al., 2008). For example, pronounced differences are seen in opioid peptide levels between rats exposed to short and long periods of maternal separation in the first 3 weeks of life, and this outcome was dependent on whether individual or litter-wise maternal separation was used (Gustafsson et al., 2008). Specifically, at 3 weeks of age, differences between animals exposed to short or long periods of maternal separation were observed in the striatum and were observed in adult rats in the ventral tegmental area and striatum. The effect seen shortly after the separation period (i.e., at 3 weeks) was particularly evident after individual maternal separation, whereas the differences seen in adult rats were noted after litter-wise separation (Gustafsson et al., 2008). These findings indicate that characteristics of early-life adversity involving the duration and degree of deprivation are important for accurately describing effects on the mesolimbic dopamine system.

Mesocortical responses to stress are notably different than mesolimbic responses, but less work has examined early-life adversity specifically in relation to the mesocortial system. As such, we first provide a brief review of general stress effects on the mesocortical system, acknowledging that these effects may vary in response to adversity experienced earlier in development.

Mesocortical dopamine neurons were reliably activated by acute, mild stressors and marked by increases in dopamine levels in the medial prefrontal cortex (mPFC), nucleus accumbens, and dorsal striatum (Abercrombie, Keefe, DiFrischia, & Zigmond, 1989; Finlay, Zigmond, & Abercrombie, 1995). Temporally, increases in dopamine release after stress induction appeared first and with greatest intensity in the mPFC, followed by the nucleus accumbens and striatum (Abercrombie et al., 1989; Chrapusta et al., 1997). Exposure to uncontrollable stressors was associated with relatively high dopamine release in the mPFC compared to exposure to controllable stressors matched for intensity and duration (Cuadra, Zurita, Lacerra, & Molina, 1999). While dopamine release in the mPFC after exposure to acute stressors occurred for animals both with and without a prior history of chronic stress exposure, mechanisms that regulated this dopamine release may operate differently. Unlike the blunting of dopamine response observed in the mesolimbic pathway after exposure to chronic stress, mesocortical dopamine reactivity to subsequent stressors appeared to be sensitized after exposure to chronic stress (Pizzagalli, 2014). For example, compared to stress-naïve animals, chronically stressed animals showed potentiated mPFC dopamine response to both novel (Cuadra et al., 1999) and familiar stressors (Chrapusta et al., 1997). Finally, mesocortical dopamine sensitization effects resulting from chronic stress exposure are enduring. Increased dopamine response in the PFC to a subsequent stressor, accompanied by attenuated response in the nucleus accumbens, has been observed 14 days after chronic exposure to footshock (Chrapusta et al., 1997), and mPFC dopamine accumulation levels exceeded control levels 14 days after chronic stress cessation (Mangiavacchi et al., 2001). Together, these findings suggest that chronic stress leads to lasting changes to mesocortical dopamine response, and these differences are manifested most strongly in the context of subsequent stressors.

The impacts of early-life adversity on the mesocortical dopamine system have not been studied extensively; however, there is evidence that dopamine function in the mPFC is altered subsequent to early-life adversity. Maternal separation has been associated with alterations to opioid peptides in the ↳ mPFC, although similar to the mesolimbic findings, the effects of early maternal separation varied as a function of separation condition (Gustafsson et al., 2008). Specifically, compared to controls, litter-separated rats had higher opioid peptide levels in the mPFC, whereas rats separated individually did not show these differences (Gustafsson et al., 2008). In an observational study of differences in naturally occurring maternal behaviors, adult rat offspring exposed to poor maternal care displayed blunting of the mPFC dopamine stress response, which was lateralized to the right hemisphere, whereas good maternal care was associated with equally attenuated mPFC dopamine stress response across both hemispheres (Zhang, Chrétien, Meaney, & Gratton, 2005). Impaired mPFC function, particularly when lateralized to the right hemisphere, has been associated with a number of stress-related pathologies (Sullivan & Gratton, 2002), as well as individual differences in positive and negative emotion (Davidson, 1998; Sullivan & Gratton, 2002; Zald, Mattson, & Pardo, 2002).

Although mPFC levels of dopamine transporter do not differ in relation to levels of maternal care, catechol-O-methyl transferase (COMT) levels, which are involved in deactivation of extracellular dopamine (Matsumoto et al., 2003), were bilaterally lower among animals exposed to below-average maternal care relative to above-average maternal care (Zhang et al., 2005). Higher levels of COMT may allow for extracellular dopamine to degrade more rapidly, resulting in smaller, shorter lasting dopamine stress responses, which have been observed in animals exposed to high, but not low, levels of maternal care (Zhang et al., 2005). Ventura and colleagues (2013) showed that unstable maternal care prevented mPFC dopamine outflow regardless of exposure to either rewarding or aversive stimuli. Combined with behavioral findings of reduced preference for sweetened fluids and impaired food place preference conditioning, disruptions to dopamine-dependent encoding of both pleasant and aversive events suggested that an unstable maternal environment may severely disrupt the propensity to seek pleasurable sources of natural rewards later in life and produce aberrant stress responses (see Ventura et al., 2013, for further discussion of the role of norepinephrine).

Summary

Disturbances to both the mesolimbic and mesocortical dopamine pathways as a result of chronic stress exposure and early-life adversity provide evidence of a direct biological pathway linking adversity to disruptions in positive emotionality. Given the hypothesized role of mesocortical dopamine neurons in inhibiting dopamine responses in the nucleus accumbens (King, Zigmond, & Finlay, 1997), sensitization of the mesocortical dopamine response may play a role in both the onset and maintenance of anhedonic symptoms associated with stressor-related psychiatric disorders (Pizzagalli, 2014) and may be linked to the higher rates of anhedonic symptoms reported among people exposed to early-life adversity (Lumley & Harkness, 2007).

Human Studies

Substantial evidence from human studies indicates that early-life adversity is associated with altered responses in the Positive Valence System across affective, behavioral, and physiological levels. These differences are evident early in life (Curtis & Cicchetti, 2013) and persist into adulthood (Young & Widom, 2014). Human studies examining disturbances to Positive Valence System domains utilize varying methodologies (described in the Key Terms and Methods section) and span broad periods of development, making synthesis of this information a complex endeavor. A number of types of early adversity have been examined in human studies, and the findings described next suggest that deficits in positive emotion processing appear to vary reliably as a function of the specific type of adversity a child experienced. As highlighted previously, we review this literature in light of a recent conceptual model of adversity that distinguishes between the dimensions of threat and deprivation (McLaughlin, 2016; McLaughlin et al., 2014; Sheridan & McLaughlin, 2014). When possible, we distinguish between exposures that reflect threat and deprivation; in studies where adversity types were not distinguished, we use the terms *maltreatment* or *adversity*.

From infancy, humans exhibit a biological preparedness to develop skills in emotion processing by learning to track associations between certain types of affective stimuli and outcomes (Pollak, 2003). Accurate recognition of facial affect depends largely on the frequency and intensity of exposure to different expressions (Beale & Keil, 1995; Keyes, 2012; Pollak, 2003). Children who have been maltreated are less likely to engage in positive interactions with their parents (Kavanagh, Youngblade, Reid, & Fagot, 1988), placing them at a disadvantage with regard to the development of skills for processing positive emotions. The identification of positive emotions involves perceptual, cognitive, and affective processes and emerges early in life (Sroufe, ↳ 1979). While emotion recognition may not be directly aligned with core Positive Valence System components, deficits in the identification of positive emotions very early in life may establish a diathesis for aberrant development of the Positive Valence System across the life span.

Children who have experienced physical and sexual abuse are more likely than nonabused children to attribute hostile intent to ambiguous social information, suggesting that they may have reduced attention to or awareness of positive cues (Dodge, Bates, & Pettit, 1990; Shields & Cicchetti, 2001), potentially due to attentional biases toward the detection of threat and anger (Pollak et al., 2000; Pollak, Messner, Kistler, & Cohn, 2009). Neglected children have more difficulty discriminating emotional expressions than non–maltreated or physically abused children, whereas physically abused children display a response bias that facilitates the identification of angry facial expressions (Pollak et al., 2000; Pollak & Sinha, 2002). More specifically, children exposed to neglect exhibited greater difficulties discriminating between sad and happy expressions than physically abused and nonmaltreated children, whereas both neglected and physically abused children showed poorer discrimination than controls between sad expressions and both neutral and fearful expressions (Pollak et al., 2000). Across infancy and childhood, institutionalized children exposed to profound levels of environmental and social deprivation did not show deficits on simple emotion recognition tasks compared to never-institutionalized children (Jeon, Moulson, Fox, Zeanah, & Nelson, 2010; Moulson, Fox, Zeanah, & Nelson, 2009; Moulson et al., 2015; C. A. Nelson, Parker, & Guthrie, 2006). However, in middle childhood, institutionalized children exhibited higher thresholds for identifying happy expressions than both family-reared and foster care children, but did not differ in their thresholds for identifying sad, angry, or fearful expressions (Moulson et al., 2015), suggesting that institutionalized children require greater perceptual information to distinguish happy from neutral expressions. In adulthood, recognition memory for positive pictures was worse among adults who experienced childhood maltreatment compared to controls, independent of psychopathology, building on evidence that early-life adversity is uniquely related to deficits in emotion processing (Masten et al., 2008; Young & Widom, 2014). These findings suggest that early-life adversity has an enduring effect on how information about positive cues is encoded, although the nature of these effects depends on type of adversity exposure.

Approach Motivation and Reward Learning

Behavioral Findings

Exposure to abuse—a marker of exposure to threat—has been reliably associated with changes in approach motivation; however, evidence for effects on reward learning is mixed. Adolescents with a history of abuse exhibited similar performance on a reward learning task (the monetary incentive delay task) as those with no abuse experiences, such that abuse history was not associated with changes in reaction times on rewarded trials relative to unrewarded trials (Dennison et al., 2016).

In a study examining performance on a reward learning task followed by an incentive-based decision-making task, an index of approach motivation, women with histories of childhood sexual abuse exhibited no differences in learning reinforcement contingencies or in using previously punished information to guide future behavior than women with no history of abuse but were less accurate when making decisions based on prior reward history (Pechtel & Pizzagalli, 2013), indicating difficulties not in reward learning when feedback was explicit, but in approach motivation. Moreover, poor performance on the incentive-based decision-making task was associated with maladaptive behaviors such as self-harm, suicidality, and risky sexual behaviors—known to be more prevalent among adolescents and adults with childhood sexual abuse histories (Danielson et al., 2010; Messman-Moore, Walsh, & DiLillo, 2010). These findings suggest that childhood sexual abuse disrupts incentive-based decision-making in adulthood and may contribute to the increased risk of engaging in maladaptive behaviors.

Alternatively, on a probabilistic reward learning task, children exposed to physical abuse were less able than nonmaltreated peers to correctly learn which stimuli predicted reward, even after repeated explicit feedback (Hanson et al., 2017). The deficits in reward learning among physically abused children were related to using information about known rewards in their environment less often and, only during the early phases of learning, making decisions as if rewards were less consistent and occurred more at random, an effect that disappeared in later trials of the task (Hanson et al., 2017). Interpreting these findings, Hanson and colleagues (2017) suggested that physically abused children have reduced expectations of rewarding events happening consistently; thus, responding variably (i.e., exploratory responding) rather than relying on environmental information (i.e., exploitative responding) may in fact be more adaptive in home environments characterized by unpredictability (Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006). The finding that expectations among physically abused children were modifiable following exposure to positive feedback provides some evidence of preserved capacity for reward learning (Hanson et al., 2017).

One possible explanation for variations in findings between studies on the association between threat exposure and reward learning may relate to unique sample characteristics regarding exposure to other forms of adversity (i.e., concurrent deprivation). None of these studies systematically controlled for deprivation, which, given the high co-occurrence of these adversities, makes it difficult to clearly identify adversity-specific effects.

There is substantial evidence to suggest that children exposed to deprivation exhibit behavioral changes in reward learning. Importantly, although there may be associations between deprivation and approach motivation, these associations have not, to our knowledge, been independently assessed due to inability to distinguish approach motivation from reward learning in most behavioral tasks. Children exposed to institutional rearing, a form of severe early deprivation, exhibited deficits in using implicit information to direct their goal-motivated behavior compared to typically developing children (Wismer Fries & Pollak, 2017). Interestingly, deficits in motivated reward learning are related to problems with indiscriminate social behaviors, which include the failure to recognize specific familiar individuals, such as caregivers, as a source of comfort and safety (Wismer Fries & Pollak, 2017). These findings, combined with the persistence of indiscriminate social behaviors after adoption, suggest that a developmentally sensitive mechanism involving poor early learning of reward contingencies may underlie these ongoing social problems.

Poor reward learning following psychosocial deprivation related to institutional rearing has been replicated. Specifically, children raised in institutions failed to modify behavioral responses and showed less accurate responding to cues associated with monetary reward, compared to typically developing children (Sheridan et al., 2018). Similarly, children given up for adoption or removed from their biological parents due to severe neglect in infancy showed deficits in using rewards to improve performance on an inhibitory control task (Mueller et al., 2012).

In a sample of children exposed to various forms of maltreatment, including both abuse and neglect, maltreatment influenced behavioral sensitivity to reward values (Guyer et al., 2006). Children exposed to various forms of maltreatment (i.e., including both abuse and neglect) failed to show sensitivity to environmental cues, such as changing reward values, to moderate their behavior (Guyer et al., 2006; Weller & Fisher, 2013). Specifically, when completing a decision-making task assessing approach motivation, maltreated children had faster overall reaction times when selecting reward contingencies than controls, but these response times did not vary as the likelihood of winning changed, whereas controls responded more quickly as the chance of winning increased. Further, failure among maltreated children to modulate behavior as the chance of winning increased was unrelated to psychopathology (Guyer et al., 2006). Compared to nonmaltreated children, maltreated children showed heightened risk-taking to avoid losses but not gains and were less able to use relative expected value of choice options to guide decision-making, but only in the context of potential losses (Weller & Fisher, 2013). Further, they were less likely to use contextual cues, such as the probability of an outcome in the face of either potential gains and losses to guide decision-making, leading to less normatively appropriate choices (Weller & Fisher, 2013). These findings could reflect a direct effect of maltreatment on approach motivation through enhanced impulsivity (Guyer et al., 2006) and reduced expectancy or sensitivity to rewards (Guyer et al., 2006; Weller & Fisher, 2013).

Neurobiological Findings

In adults, childhood abuse has been associated with weaker responses in the left pallidum and left putamen during anticipation of monetary reward (Dillon et al., 2009), although these effects could not be clearly distinguished from the experience of psychopathology. Compared to psychiatric controls, women with a history of childhood sexual abuse showed increased subgenual anterior cingulate activation when making decisions reliant on information about previously learned reward contingencies (Pechtel & Pizzagalli, 2013). Given the role of the anterior cingulate in emotional responding and evaluation of feedback salience (M. L. Phillips, Drevets, Rauch, & Lane, 2003; Pizzagalli, 2011), Pechtel and Pizzagalli (2013) speculated that the experience of childhood sexual abuse could lead to higher levels of emotional arousal in the context of incentive-based decision-making, which may, in turn, interfere with adaptive decision-making and contribute to increased risk for engaging in maladaptive ↳ behavior observed in this population. Similarly, in a small sample of adolescents, severe institutional deprivation in early childhood was associated with hyporesponsiveness in the ventral striatum and the caudate during anticipation of monetary reward (Mehta et al., 2010), but again, these effects could not be distinguished from current psychopathology. In healthy young adults, early exposure to poverty and social disadvantage was associated with reduced neural reactivity in the ventral and dorsal striatum during anticipation of reward (Boecker et al., 2014). These neurobiological studies suggest that various forms of adversity are associated with weaker neurobiological responses in the context of anticipating rewards, but neurobiological correlates of reward learning are less clear.

Initial and Sustained Responsiveness to Reward

Subjective Affect

In a cross-sectional study of adults, childhood abuse was associated with less positive ratings of neutral cues paired with reward (Dillon et al., 2009). However, given high rates of psychopathology in this sample, determining the direct effect of adversity on initial responsiveness to reward independent of current or lifetime history of depression was not possible (Dillon et al., 2009). In contrast, adolescents who were abused did not rate positive social images differently than controls (Dennison et al., 2016). Similarly, in a sample of maltreated children, subjective affective ratings of neutral cues associated with reward did not vary by adversity exposure (Guyer et al., 2006), suggesting that maltreated children "like" rewarded cues as much as nonmaltreated children.

Neurobiological Findings

Evidence from both EEG and fMRI studies suggest that the nature of neurobiological response to rewarding or positive cues varies in response to experiences of threat and deprivation, highlighting the need for more systematic examination of these environmental variables. fMRI studies have reported mixed findings regarding adversity-related differences in neural responses on initial receipt of monetary reward or viewing positive images. Adolescents with abuse histories showed heightened reactivity in the nucleus accumbens and putamen when viewing positive social stimuli (Dennison et al., 2016). This pattern might be explained by the fact that children who have been abused typically live in environments characterized by low levels of positive affect and warmth (Bugental, Blue, & Lewis, 1990; Burgess & Conger, 1978; Kavanagh et al., 1988); thus, the experience of positive social cues may be more unexpected or surprising for these children. Indeed, nucleus accumbens response to reward receipt was magnified when rewards were unexpected or surprising (Berns, McClure, Pagnoni, & Montague, 2001), and putamen activity was associated with detecting behaviors that predicted unexpected changes in reward outcomes (Haruno & Kawato, 2006). A similar pattern has been observed in healthy young adults, such that early exposure to poverty and social disadvantage was associated with heightened reactivity during monetary reward delivery in the putamen, right pallidum, and insula (Boecker et al., 2014). Alternatively, in early adulthood, the experience of emotional neglect (but not physical neglect or any form of abuse) in childhood has been associated with *blunted* development of activity in the ventral striatum on receipt of monetary reward (Hanson, Hariri, & Williamson, 2015).[1] Similarly, in a sample of postinstitutionalized adolescents, institutionalization was associated with blunted development of reactivity to happy faces in the ventral striatum (Goff et al., 2013).

In 15-month-old infants, both P1 and Nc amplitude—indices of sensory and attentional processes, respectively—were greater among maltreated infants in response to happy facial expressions compared to angry faces, whereas nonmaltreated children exhibited greater amplitude to angry faces compared to happy faces (Curtis & Cicchetti, 2013). These differences indicated sensitivity to novel facial ↳ stimuli (Hernandez-Reif, Field, Diego, Vera, & Pickens, 2006), reflective of differences in the infants' emotional milieu: Maltreated infants are less likely to experience positive facial expressions, whereas nonmaltreated children are likely to be less familiar with angry faces (Kavanagh et al., 1988; Malatesta & Haviland, 1982). In contrast, at 30 months, maltreated children showed greater amplitude of the Nc waveform while viewing angry faces relative to happy and neutral faces, which may reflect, by this stage of development, greater familiarity with threatening cues among maltreated children (Carver et al., 2003; Cicchetti & Curtis, 2005; de Haan, Johnson, & Halit, 2007; Grossmann, Striano, & Friederici, 2007). By 42 months of age, maltreated children had greater P1 amplitude to angry faces compared to both happy faces and nonmaltreated children (Curtis & Cicchetti, 2011). This pattern of greater reactivity to threatening cues among maltreated children persists, with similar findings reported in other studies of school-aged children examining the P3b amplitude, which is associated with active cognitive processing (Pollak, Cicchetti, Klorman, & Brumaghim, 1997; Pollak, Klorman, Thatcher, & Cicchetti, 2001). Curtis and Cicchetti (2013) hypothesized that this developmental shift correlated with changes in the child's level of agency and autonomy (i.e., expressions of will, greater locomotive ability) that are likely to be experienced as more challenging for parents of maltreated children, eliciting more anger, leading the child to learn an association between angry facial affect and negative consequences, contributing to a shift toward the increasing salience of angry facial affect.

Children aged 6 to 12 years who experienced physical abuse, neglect, or both exhibited no differences in ERPs compared to controls when identifying happy faces as targets in a simple emotion-processing task (Pollak et al., 2001). However, maltreated children exhibited heightened P3b amplitudes, an index of increased attentional resources, compared to nonmaltreated children when angry, but not happy, faces were targets. Given that this sample included children exposed to both threat and deprivation, and in light of other evidence that the effects of these adversity types may vary, it is difficult to distinguish between the possibility that there are no differences in allocation of attentional resources when processing positive emotional stimuli as a function of specific types of adversity or whether the ERP effects observed earlier in development "normalize" later in development.

Mixed findings in subjective and biological responses to receipt of reward indicate further need to examine developmental differences in initial responsiveness to reward and to carefully consider how the dimensions of threat and deprivation described may differentially influence these unique aspects of positive emotion processing. We are unaware of any studies that have clearly examined associations between sustained responsiveness to reward and early-life adversity.

Expression and Experience of Positive Emotions

Although expression of positive emotion does not align clearly with a specific domain of Positive Valence System functioning, expression is an important area of positive emotionality that is clearly influenced by early-life adversity. Childhood experiences of threat and deprivation are consistently associated with decreased expression of positive emotion. Children who are abused by their parents showed less positive emotion and more negative emotion (Bugental et al., 1990; Kavanagh et al., 1988). Children exposed to deprived institutional rearing displayed deficits in expressing positive affect in very early childhood (Smyke et al., 2007) that were maintained with ongoing institutionalized care (Ghera et al., 2009). Indeed, the regimen of institutional care may provide children with limited opportunities to experience contingent caregiving and the positive reinforcement necessary for developing knowledge about reward-related contingencies. For example, they may lack knowledge about self-initiated behavioral repertoires that elicit positive experiences from their environment, which may produce global deficits in the subjective experience and expression of positive emotions. In a study of postinstitutionalized children, differences in self-reported positive emotion were not evident in late childhood but were lower than controls in adolescence, suggesting that the impacts of early-life deprivation may, in some cases, be delayed (Goff et al., 2013).

A recent study showed that "street boys" raised largely without parental or social care in postconflict Sierra Leone exhibited reduced facial mimicry of both positive and negative emotions (Ardizzi et al., 2013). Facial mimicry is an instrumental component of social communication (i.e., empathy) that emerges early in infancy and is fostered by secure attachment (Dykas, Ehrlich, & Cassidy, 2011) and positive reinforcement (Sims, Van Reekum, Johnstone, & Chakrabarti, 2012). Adults with maltreatment histories also reported lower levels of ↳ positive emotion (Dillon et al., 2009), but this finding has not been clearly distinguished from co-occurring psychopathology. p. 512

Neural Structure in Dopamine-Related Regions

There are very few studies examining adversity-related structural differences in dopamine-related brain regions, particularly in abused populations. Compared to nonabused controls, adults with histories of childhood abuse did not show any differences in basal ganglia volumes (Dillon et al., 2009). Institutional rearing has been associated with alterations in the development of white matter tracts linked with positive emotion (Bick et al., 2015). Specifically, between 8 and 10 years of age, institutionally raised children showed poorer white matter integrity in the external capsule, and reduced integrity of this region has been associated with addiction disorders during adolescence (Bick et al., 2015; Lin et al., 2012). Positively, alterations in white matter integrity of the external capsule were somewhat remediated in children who had been removed from institutional care and placed in supported foster care (Bick et al., 2015). Further, neglect-related alterations in the external capsule partially explained links between institutional rearing status and internalizing symptoms in middle childhood and adolescence (Bick, Fox, Zeanah, & Nelson, 2017). In a sample derived from the same study (Bucharest Early Intervention Project), Sheridan and colleagues (2018) observed that relative to children randomly assigned to a foster care intervention, children who remained in institutions longer had a thicker dorsal ACC, a neurodevelopmental marker associated with poorer reward learning, but showed no differences in orbital cortex thickness or striatal volume. As cortical gray matter typically thins with age (Gogtay et al., 2004; Raznahan et al., 2011), a thicker dorsal ACC in institutionalized children may reflect less mature development of this region, potentially contributing to disruptions in reward learning.

Summary

In an environment characterized by atypical levels of threat, cues that signal danger are likely to possess greater familiarity (Cicchetti & Curtis, 2005), salience (Pollak et al., 2009), and importance than positive emotional cues (McLaughlin, Peverill, Gold, Alves, & Sheridan, 2015). In this way, resources typically allocated to seeking and enjoying rewards may be sacrificed for learning contingencies that promote immediate adaptation to threat. In contrast, exposure to highly deprived environments characterized by a lack of emotionally informative stimuli was associated with poor reward learning ability and indiscriminant, dampened responses to all emotional expressions (i.e., global cortical hypoarousal; see Marshall & Fox, 2004; Marshall, Reeb, Fox, Nelson, & Zeanah, 2008; Moulson et al., 2009).

Given that changes resulting from early-life adversity occur during a rapid and ongoing neurodevelopmental period, the impacts on the development of positive emotion are likely to be lasting, changing the course of subsequent development (Goff et al., 2013; Whittle et al., 2013). Differences in emotion processing and neurodevelopment arising from early-life adversity do not typically present as disorder-level difficulties with positive emotion by late childhood. However, these patterns may interact with subsequent development of neurobiological systems during adolescence—a time of significant developmental reorganization of the neurobiological systems underlying positive emotion (Spear, 2000)—to create the observed increased risk for disorders of positive emotion among adolescents and adults who have experienced early-life adversity (Dube et al., 2003; Green et al., 2010; Widom, 1999; Widom et al., 2007).

Protector: Positive Emotionality as a Moderator of Risk for Psychopathology Following Adversity

While early-life adversity is a potent risk factor for disorders of positive emotion, not all children exposed to adversity go on to experience mental health problems as adults (Collishaw et al., 2007). For example, in a sample of adults who had experienced repeated, ongoing, or severe sexual or physical abuse as children, a substantial majority (43.5 percent) reported no psychiatric disorders or suicidality over a 30-year follow-up period into adulthood (Collishaw et al., 2007). In this early study, a number of factors were related to resilience: perceived parental care, adolescent peer relationships, the quality of adult love relationships, and personality style (Collishaw et al., 2007).

Since this early study of resilience following early-life adversity, a growing literature has shown that positive emotions appear to buffer against risk for psychopathology following traumatic events or adversity in adulthood (Folkman, 2008; Fredrickson, Tugade, Waugh, & Larkin, 2003; Tugade & Fredrickson, 2004). For example, positive emotions have been associated with resilience to stressful events in adulthood, and the experience of positive emotions exhibited protective effects operating at ↳ both physiological and psychological levels (for reviews, see Folkman, 2008; Lyubomirsky, King, & Diener, 2005; Pressman & Cohen, 2005; Southwick, Vythilingam, & Charney, 2005). Here, we discuss evidence that individual differences in the Positive Valence System may confer risk and resilience to adverse effects associated with early-life adversity.

Studies examining the protective effects of positive emotionality following early-life adversity have emerged recently. Although a number of studies have conceptualized reactivity to rewards (money, positive social stimuli) as mediators of the association between early-life adversity and psychopathology (Boecker et al., 2014; Goff et al., 2013; Hanson et al., 2015, 2017; Sheridan et al., 2018), evidence for such mediation is mixed. In a large sample of university students, decreased behavioral and neural responses in the ventral striatum to monetary reward across adolescence mediated the association of emotional neglect with depression (Hanson et al., 2015),[2] although variation in exposure to neglect in this population was restricted. Impaired associative (reward) learning partially explained higher levels of behavioral problems among youth exposed to physical abuse earlier in childhood (Hanson et al., 2017). Among institutionalized children, accuracy on a reward learning task mediated increased risk for depressive symptoms associated with prolonged institutionalization (Sheridan et al., 2018). However, no evidence for the mediating role of neuronal responses to positive social stimuli on the association between early adversity and psychopathology has been found in children and adolescents with histories of early-life institutionalization (Goff et al., 2013) or in young adults exposed to poverty and social disadvantage early in life (Boecker et al., 2014). A starting point to clarify these mixed findings could involve more systematic operationalization of Positive Valence System constructs that may exert unique effects (PVS Workgroup, 2011); for example, accuracy on a reward learning task may relate to the reward learning domain, whereas neuronal responses to passively viewed positive social stimuli indicate initial responsiveness to reward attainment.

An alternative possibility explaining these contradictory findings is that individual variation in positive emotion, or particular subdomains, moderates the association of adversity with psychopathology. Specifically, stable individual differences in positive emotion, possibly indexed by temperamental factors, emerge early in development (Compas, Connor-Smith, & Jaser, 2004), producing individual differences in risk for psychopathology following exposure to early-life adversity. Higher levels of trait positive affect buffer risk for depression among children with high negative emotion (Joiner & Lonigan, 2000) and protect against adjustment problems following parental divorce (Lengua, Wolchik, Sandler, & West, 2000). In a study examining the role of temperament as a predictor of children’s appraisal, coping styles, and adjustment problems, positive emotionality was surprisingly not related to positive appraisal or active coping but did predict lower adjustment problems independently of those variables (Lengua & Long, 2002).

Further, positive emotionality was not related to negative life events, suggesting that as an individual characteristic, it may be impervious to stress (Lengua & Long, 2002); indeed, heritability for positive emotionality was estimated to be between 40 and 50 percent (Sprangers et al., 2010).

There is conjecture about Lengua and Long's (2002) findings, which appear at odds with research in adults demonstrating that positive emotionality promoted positive appraisal and adaptive coping in the face of stressful events (Folkman, 2008). On one hand, Lengua and Long (2002) suggested their findings may relate to the measurement of positive emotionality assessed using "smiling" and "laughing" behaviors, rather than approach behaviors and extraversion (Lengua & Long, 2002). Interestingly, positive emotionality measured in this way is consistent with initial responsiveness to reward attainment, capturing autonomic, biologically driven, stable reactivity to pleasant events, which have been associated with resilience to early-life adversity (Corral-Frias et al., 2015; Dennison et al., 2016). On the other hand, approach behaviors and extraversion are only likely to be adaptive responses to adverse events when *contextual factors* surrounding the event are considered. For example, a child who indiscriminately continues to approach an abusive caregiver is more often likely to be punished rather than rewarded. Adaptive use of approach behaviors is likely to require self-regulation, which has been shown to predict fewer negative life events, active coping, and fewer adjustment problems in children (Lengua & Long, 2002; Thompson, Lengua, & Garcia, 2016; Thompson, Zalewski, & Lengua, 2014). In this way, positive emotionality, assessed as initial responsiveness to pleasant events but not approach motivation, may play a protective role independent of self-regulation (i.e., the stress–appraisal–coping process) (Lengua & Long, 2002).

p. 514 In two related studies involving samples of young adult university students, increased reactivity of the ventral striatum to receipt of reward (i.e., initial response to reward) buffered against anhedonia symptoms following stressful life events (Nikolova, Bogdan, Brigidi, & Hariri, 2012) and early-life stress (Corral-Frias et al., 2015), suggesting that higher initial responsiveness to reward might buffer against the development of depression following both early-life and recent stressful experiences. Although the findings reported by Corral-Frias and colleagues (2015) provided some support for the role of initial responsiveness in resilience to depression following early-life stress, the sample comprised a population of comparatively high-functioning adults (i.e., university students) with low exposure to early-life stress, measured as an aggregate of threat and deprivation exposure, and rates of depression well below population levels (Kessler et al., 2005; Merikangas et al., 2010). A recent study replicated these findings among adolescents with exposure to high levels of abuse, indicating a moderating role of reactivity to positive and rewarding cues across behavioral and neurobiological measures in the association between childhood abuse and depression (Dennison et al., 2016). Specifically, abused youths who exhibited faster reaction time to cues paired with monetary reward relative to those unpaired with reward, and greater BOLD signal in the left pallidum to positive pictures compared to neutral pictures, are protected against symptoms of depression compared to abused youth with low reactivity to reward. Longitudinally, greater BOLD signal in the left putamen to positive images moderated the association of abuse with change in depression scores over time, such that higher levels of reward response were associated with lower increases in depression over time among abused youths (Dennison et al., 2016). The neurobiological findings provided evidence that initial responsiveness to reward attainment moderated the association between childhood abuse and adolescent depression. The behavioral findings were less clear: Relatively faster reaction times on rewarded versus nonrewarded trials could indicate either heightened approach motivation or better reward learning, or both together, protect against depression following childhood abuse.

Why might initial responsiveness to positive environmental cues and rewarding events be associated with resilience to depressive symptomology following early-life adversity? Dopamine release is observed in both the ventral and dorsal striatum on receipt of rewards (Breiter et al., 1997; Koepp et al., 1998), and the dorsal striatum plays a specific role in learning stimulus–response contingencies necessary for appetitive behavior (Mannella, Gurney, & Baldassarre, 2013; O'Doherty et al., 2004). Animal studies indicated putamen inactivation caused an inability to maintain or learn habitual responses to rewards (Yin, Knowlton, & Balleine, 2004). The acquisition of an appetitive behavior prior to stress exposure in rodents protected against stress-induced changes to dopamine transmission in the mesolimbic pathway (Nanni et al., 2003), consistent with the finding that greater putamen activation buffered risk for future depression among abused adolescents (Dennison et al., 2016).

There is evidence from animal studies that positive emotionality, indexed at both the neurological and behavioral levels, may moderate the association between adverse events and coping failure. It is worth noting that none of these studies described resilience to early-life adversity because they were conducted in adult animals. In adult rats, enhanced mesolimbic dopamine release in the face of acute, but not prolonged or uncontrollable, stressors promoted behavioral activation and active coping (Cabib & Puglisi-Allegra, 2012). Mice that exhibited resilience to social defeat stress were characterized by increased plasticity and gene expression within key nodes of the reward network: the ventral tegmental area and nucleus accumbens (Krishnan et al., 2007). One innovative study classified rats into trait "optimistic" and "pessimistic" groups using an ambiguous cue interpretation test, showing that after exposure to physical restraint both groups exhibited anhedonia, but it occurred faster and lasted longer in "pessmistic" compared to "optimistic" rats (Rygula, Papciak, & Popik, 2013). Although chronic stress exposure increased negative judgment bias in all rats independent of trait pessimism (Rygula et al., 2013), these findings are consistent with evidence that resilience is not marked by the absence of negative emotions. Rather, resilience appears to be marked by the ability to experience positive emotions in stressful contexts, which is thought to facilitate better coping and faster recovery (Folkman, 2008).

Early findings from both human and animal studies suggested that the ability to maintain initial responsiveness to positive events was a potential marker of resilience to psychopathology subsequent to early-life adversity, particularly for depression. Evidence for the protective roles of approach motivation, reward learning, and sustained responsiveness is less clear and requires more thorough investigation. Moreover, although enhanced initial responsiveness to reward may confer protection against depression, the associations with substance abuse or other risk behaviors have yet to be investigated. These initial findings highlight an important role for individual differences in positive emotionality as a core neurodevelopmental mechanism in the etiology of psychopathology following early-life adversity. It remains unknown whether positive emotionality differentially moderates the association between different types of early-life adversity (i.e., threat vs. deprivation, acute or chronic) and psychopathology.

Future Directions and Clinical Implications

Childhood maltreatment is associated with poorer responses to standard treatments for common mental health problems, including depression (Nanni et al., 2012), highlighting the need for alternative treatments in this vulnerable population. Correlates of resilience provide potential targets for therapeutic innovation. Findings that the acquisition of an appetitive behavior prior to stress exposure can prevent stress-induced depletion in dopamine output (Nanni et al., 2003) suggest that treatments that promote instrumental learning about rewards, such as behavioral activation (Dimidjian et al., 2006), might be particularly effective in treating or preventing psychopathology associated with early-life adversity. We are unaware of intervention studies examining this possibility.

Given variability in the associations between different types of adverse experiences and their impacts on the positive emotion system, greater specificity in defining these experiences may provide much-needed insight into the underlying mechanisms linking early-life stress exposure to psychopathology. Examining the unique contributions of adversity along dimensions of threat and deprivation will help us understand how these unique experiences shape both behavioral and neurological development. Given the high co-occurrence of adverse experiences (McLaughlin et al., 2012), other multivariate techniques are not likely to shed light on specificity. Given this, animal studies that consider the effects of early-life exposure to threat in the absence of deprivation (i.e., short-term exposure to footshock without maternal/sibling separation) will be instrumental in understanding unique effects of these different types of exposure. A further limitation relates to describing the effects of severity, developmental timing, and duration of adverse experiences, particularly given animal studies have shown important differences along these dimensions. More descriptive classification will help us better understand developmental mechanisms linking adversity, disruptions to positive emotionality, and psychopathology, ultimately informing the development of novel intervention approaches.

This chapter also highlights the need for future studies to more systematically approach the measurement of positive emotionality by considering the distinct aspects of Positive Valence System function. We suggest that the four Positive Valence System constructs (Table 29.1) provide a conceptually coherent framework for both implementing existing and developing novel reward tasks to precisely measure these constructs. For example, while both Goff et al. (2013) and Hanson et al. (2015) reported that deprivation-related adversity was associated developmentally blunted responsiveness in the nucleus accumbens on reward receipt, further analyses of these data separating early versus late trials may shed light on whether these blunted effects are observed both initially and over time and thus more clearly disentangle initial from sustained responsiveness (see Heller et al., 2009). Similarly, more comprehensive assessment of behavioral responses to reward using stochastic, rather than fixed, learning tasks will help further disentangle reward learning from approach motivation (Hanson et al., 2017).

Conclusion

Early-life adversity is associated with disruptions to the Positive Valence System across behavioral, neural, and psychological levels, and it is likely that these disturbances are involved in the onset of psychopathology. However, the impact of early-life adversity appears to be moderated by behavioral and neurological markers of positive emotionality: A greater propensity to experience positive emotions when positive events happen is associated with greater resilience following early-life adversity. In turn, increased initial responsiveness to rewards may promote greater expectancy and desire to seek positive stimuli from the environment. Further research is needed to understand the nature of these protective effects in relation to subcomponents of the Positive Valence System and to identify under which conditions protective factors provide the most benefit following early-life adversity. This important correlate of resilience provides a potential target for developing more effective treatments for individuals with histories of early-life adversity.

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Notes

1 Hanson et al. (2015) measured emotional neglect using the Childhood Trauma Questionnaire (CTQ). We would argue that the Emotional Neglect scale from the CTQ is an inadequate measure of adversity relating to neglect. First, this subscale is

composed entirely of positively framed questions that assess family cohesion (e.g., “People in my family felt close to each other,” “There was someone in my family who made me feel important or special”) that are reverse scored. These items capture the quality or closeness of relationships between parents and children, but reverse scoring them does not provide a conceptually valid or direct measure of neglect; there are many reasons that people might report not feeling close to people in their family in situations that do not resemble or even approximate neglect. Second, given the interpersonal nature of these items, we would argue that this subscale is particularly susceptible to cognitive and affective biases associated with current psychopathology (Brewin, Andrews, & Gotlib, 1993; Joormann & Gotlib, 2006; Koster, De Raedt, Leyman, & De Lissnyder, 2010; Leyman, De Raedt, Schacht, & Koster, 2007), the outcome measure in this study. We would recommend that emotional neglect is more reliably measured using structured interviews, such as the Childhood Experience of Care and Abuse (Bifulco, Brown, Lillie, & Jarvis, 1997).

2 See Note 1.