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The Role of Parenting in the Emergence of Human Emotion: New Approaches to the Old Nature-Nurture Debate

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SYNOPSIS

Emotions are complex processes that are essential for survival and adaptation. Recent studies of children and animals are shedding light on how the developing brain learns to rapidly respond to signals in the environment, assess the emotional significance of this information, and in so doing adaptively regulate subsequent behavior. Here, I describe studies of children and nonhuman primates who are developing within emotionally aberrant environments. Examining these populations provides new insights on the ways in which the social or interpersonal contexts of parenting may influence development of the neural systems underlying emotional behavior.

INTRODUCTION

Application of Developmental Affective Neuroscience Approaches to Issues About Parenting

The traditional view of the origins of emotions maintains that humans are genetically programmed to develop the circuitry that underlies basic emotional behaviors. Darwin (1872/1965), for example, argued that facial expressions are innate. By describing emotions as innate, Darwin meant that the ability to pose, express, and understand the meaning of facial expressions exists in the brain independent of any kind of sensory or learning experience. The contrasting view holds that the brain does not contain innate knowledge of emotions or specific packages of skills; instead, humans possess inborn capabilities for learning from the environment. This concept emphasizes the role of sensory experience as the basis of emotional development. Ultimately, what we really need to understand, if we wish to translate basic science into interventions for maladaptive behaviors, is *how* change occurs. How does the individual child learn how to engage in effective emotional communication?

Over the course of development, for most children, emotional and behavioral systems and the unfolding of neurobiological development interact seamlessly with the contingency structure of the social environment. However, underlying these complex behaviors are myriad skills that are necessary for successful adaptation to novel experiences and to the dynamic social contexts in which children develop. These skills include encoding and conveying emotional and behavioral signals among caregivers, peers, and persons in the wider social contexts. Adaptation to these varied contexts reflects rapid and complex learning. These emotional and behavioral learning processes become increasingly intricate as relevant neuroanatomical and neurobiological systems develop. This pattern of development suggests that more sophisticated emotional and behavioral skills rely on the organization of relevant neural substrates in relation to experience. Understanding the processes underlying neurobiological functioning across developmental epochs will stimulate the development of new prevention and intervention efforts to foster effective parenting processes for at-risk children. For example, harsh and inconsistent parenting has

been repeatedly shown to foster risk for emotion regulation problems. Yet major questions remain about the exact processes through which children's early social environments affect the neurobiological mechanisms underlying social behaviors (Pollak, 2005). Innovative new technologies play a major role in facilitating the application of theory-based analyses at levels of the brain, biology, and behavior.

My students and I have employed psychophysiological methods such as structural and functional magnetic resonance imaging (MRI) and event-related potential (ERP) to identify areas and functions of the brain linked to social experiences such as parental maltreatment of school-aged children. To investigate whether maltreatment was related to structural brain changes, detailed anatomical images have been gained through structural MRI studies. For example, the orbitofrontal cortex (oFC) is deeply involved in learning social cues, and therefore has important implications for socio-emotional development and behavioral regulation (Bachevalier & Loveland, 2006). The protracted development of the oFC suggests that it may be particularly vulnerable to post-natal experience. Our MRI data revealed that maltreated adolescents had smaller oFC volumes compared to non-maltreated adolescents, and that the size of the child's oFC region predicted the amount of stress that children reported (Hanson et al., 2010). In another MRI study, we examined the question of whether there were structural brain differences in adolescents based on early caregiving experiences (Bauer, Hanson, Pierson, Davidson, & Pollak, 2009). This study was prompted by the social and behavioral deficits demonstrated by post-institutionalized children. Here, we focused specifically on the cerebellum. The cerebellum is a brain region that is highly influenced by experience rather than genetic endowment (Giedd, Schmitt, & Neale, 2007). We found that the posterior-superior lobe of the cerebellum was smaller in the post-institutionalized children as compared to typically developing children. This region was also associated with children's performance on a task of executive function in that children with a smaller superior-posterior lobe volume showed poor executive control (Bauer et al., 2009). The results of this and other studies (Pollak, 2005, 2008) suggest a mechanism by which the early experience of deprivation could exert lasting consequences on social regulation.

Insights into the processes involved in emotion regulation have been facilitated by the study of electrophysiology in at-risk children. This psychophysiological method helps measure children's attention to and processing of social information. Evidence from ERP studies suggests that physically abused and typically developing children have differences in their neural responses to anger. For example, physically abused children are reared in an environment in which anger is an extremely salient cue. It is highly predictive of danger and, as such, it is adaptive for the child to be sensitized to this signal. Indeed, we have demonstrated that 4-6 year-old children who experience physical abuse more quickly identify anger than typically developing children (Pollak, Cicchetti, Hornung, & Reed, 2000). However, the behavioral studies alone do not provide any evidence indicating how this enhanced perceptual ability serves as a risk factor for children. We hypothesized that these behavioral features meant that physically abused children were devoting disproportionate cognitive resources to signals of anger. Such privileged processing of anger might deflect resources from other important cognitive and emotional processes necessary for healthy social functioning. To test this hypothesis, we used an electrophysiological approach called the event-related potential (ERP). An ERP is averaged electroencephalogram (EEG) data that are time-locked to specific stimuli. As such, ERPs can be used as an index of various cognitive processes including attention. A specific aspect of the ERP, the P3b component, is thought to reflect selective attention toward task-relevant information. As expected, physically abused school-aged children showed an enhanced P3b in response to angry faces compared to other emotions (Pollak, Cicchetti, Klorman, & Brumaghim, 1997; Pollak, Klorman, Thatcher, & Cicchetti, 2001). Further, using the P3b as an index of attention, we observed that physically abused school-aged children showed

enhanced attentional allocation toward vocal expressions of anger and P3b amplitude in response to anger was associated with severity of physical maltreatment (Shackman, Shackman, & Pollak, 2007). Maltreated children also have difficulty disengaging attention from angry faces (Pollak & Tolley-Schell, 2003) and show impaired regulation of goal-directed attention (Shackman et al., 2007). Research using the N2 ERP component, an index of conflict processing, also revealed that physically abused children attend to facial signals of anger even when instructed to ignore them (Shackman et al., 2007) and that the degree of cognitive conflict experienced in response to task-irrelevant angry faces predicts poorer task performance. In this series of investigations, ERPs provided insight into an aspect of maltreated children's social development-- attention to anger-- something that could not have been observed by behavioral methods alone. The severity of the maltreatment predicted attention to anger, and the more attention devoted to anger, the worse the children performed on the task.

The addition of endocrine measures to other psychophysiological methods allows us to index active regulatory processes in children. Endocrine systems play an important role in the regulation of social behavior, and animal studies have provided a great deal of evidence that the endocrine system can be altered through early experience (Sanchez et al., 2005). We have examined the effects of early adverse experience on the neuropeptide oxytocin and the stress-related hormone cortisol. Oxytocin is a polypeptide hormone and neuroregulator produced in the hypothalamus and released centrally and peripherally into the blood stream via axon terminals in the posterior pituitary. It appears to be part of the neural system of reward circuitry that includes the nucleus accumbens (Lovic & Fleming, 2004). For example, in nonhuman animals and humans alike, higher levels of oxytocin are associated with decreases in stress hormones, such as cortisol, as well as with increased positive behaviors of social interaction and attachment (Grippe, Trahanas, Zimmerman, Porges, & Carter, 2009).

Oxytocin and cortisol are both affected by adverse rearing conditions. Cortisol, the end product of the HPA axis, modulates a wide range of biological responses such as energy release, cardiovascular function, immune activity, growth, emotion, and cognition (Sapolsky, Romero, & Munck, 2000). Secretion of cortisol allows the organism to regulate metabolic processes, and to adapt and cope effectively with current stressors. However, chronic elevation of cortisol impairs behavioral adaptation and has been associated with emotion regulation and behavior regulation difficulties as well as with psychopathology (Sapolsky et al., 2000). The behavioral problems of post-institutionalized children are consistent with dysregulation in the oxytocin system and the HPA axis. To examine this, Wismer Fries and colleagues investigated toddlers' oxytocin and cortisol levels in response to a social game with their mother and with a stranger. This investigation demonstrated that, unlike typically developing children, post-institutionalized children have an abnormally suppressed oxytocin response after interacting with their adoptive mothers (Wismer Fries, Ziegler, Kurian, Jacoris, & Pollak, 2005). Further, post-institutionalized toddlers showed prolonged elevations in cortisol levels following the interaction with their adoptive mother, but not with the stranger. More severe neglect was associated with the highest basal cortisol levels. The more severely neglected children also had the most impaired cortisol regulation following the mother interaction (Wismer Fries, Shirtcliff, & Pollak, 2008). These results suggest that early social deprivation may disrupt the function of the oxytocin system and HPA axis. This use of hormone measures, therefore, suggests that these children's interactions may not be calming and comforting because these children's neuro-hormonal systems do not respond in an adaptive manner. If this is indeed the case, it is easy to infer how such experiences could interfere with the development of adaptive social relationships.

INPUT AND LEARNING: WHAT DO THE EMOTIONAL CORRELATES OF CHILD MALTREATMENT TEACH US ABOUT PARENTING?

Early Emotional Input Has Important, Cascading Effects

Parents who physically abuse and/or neglect their children have been characterized by increased hostility, generally negative parenting techniques, and poorly expressed emotions (Lesnik-Oberstein, Koers, & Cohen, 1995). However, there is little detailed empirical data on this type of expressive environment. We evaluated the facial and vocal expressions of a sample of physically abusive and nonabusive mothers and found that abusive mothers produced atypical and less recognizable expressions of anger (Shackman et al., 2010). For example, physically abusive mothers did not lower and contract their brows as most people do when angry, tended to smile less intensely, and produced lower levels of vocal emotions that lacked variation in pitch. These data suggest that physically abused children may be exposed to less prototypical emotional expressions in their early sensory environments. The implication of the Shackman and colleagues (2010) study is that whatever kind of developmental mechanism children use to learn about emotion is likely to be affected by degraded input. Typically, adults exaggerate sensory input to facilitate infant learning. For example, infant-directed speech, which is characterized by a higher fundamental frequency and greater pitch variations, is thought to facilitate infants' language learning (Thiessen, Hill, & Saffran, 2005). Similarly, adults often present infants with high-contrast toys and mobiles to stimulate visual development. If maltreated children are exposed to degraded emotional input—meaning that the quality of the signals they receive are less clear, inconsistent, and more difficult to understand—then it is not surprising that emotion learning could be compromised.

Perceptual Mechanisms Respond to Emotional Input

Given that maltreated children may encounter variations in their emotional input, it is possible that children's early experiences alter sensory thresholds for emotion. To explore this possibility as a learning mechanism for emotion, we examined how children categorize emotions. It appears that human infants enter the world with general perceptual learning mechanisms that allow them to conduct a preliminary analysis of their environments, but these mechanisms must become tuned to process specific aspects of the environment (Aslin, Jusczyk, & Pisoni, 1998). When shown facial expressions distributed along a continuum between emotions (e.g., happiness to sadness), adults perceive these stimuli as belonging to discrete emotion categories (e.g., happiness or sadness) (Young et al., 1997). Furthermore, category boundaries for familiar and unfamiliar faces can be shifted in adults as a function of frequency of exposure to those faces (Beale & Kiel, 1995). This frequency effect suggests that experience may also play an important role in facial perception. To determine if a frequency effect for emotions could also be detected, we examined physically abused children's categorical perception of emotional expressions and found that, while all the children we studied perceived emotions in terms of categories (e.g., sad, angry, happy, scared), physically abused children displayed a boundary shift for perceptual categories of anger relative to nonmaltreated children (Pollak & Kistler, 2002). Specifically, physically abused children displayed equivalent category boundaries to nonabused children when discriminating continua of happiness blended into fear and sadness. However, these same children evinced different category boundaries when discriminating angry faces blended into either fear or sadness. These data suggest an effect of learning on the formation of perceptual representations of emotion and, given that categorical perceptual mechanisms appear to operate similarly across domains and various species (including humans, birds, and chinchillas), that this process may reflect a domain-general learning mechanism subserving emotional development.

Cognitive Mechanisms Respond to Emotional Input

Children's deployment and control of attention represents another way in which to examine the role of learning in emotional development. The adaptive nature of involuntary (or reflex-like) allocation of attention lies in its ability to quickly alert an organism to a possible danger or other significant event. Voluntary (or controlled, intentional) allocation of attention toward or away from certain environmental cues is a mechanism that allows children to effectively regulate emotional states. To examine the ways in which early emotional experience affects voluntary and involuntary attention, we manipulated the task relevance of conflicting affective cues and used ERPs to measure physically abused children's cognitive processing. We presented school-aged children with congruent and incongruent facial and vocal emotion expressions while directing their attention toward either the visual or auditory modality. In general, we found that physically abused children (1) exhibited increased voluntary attention toward both facial and vocal anger cues, (2) were involuntarily drawn to vocal anger cues, and (3) were especially responsive to facial signals of anger from their own parent (Shackman, Shackman, & Pollak, 2007). Physically abused children showed enhanced P3b amplitude when directing their attention to their own mother's facial anger. The groups of abused and control children did not differ when attending to anger posed by unfamiliar adults, or when attending to happy and sad facial expressions posed by either their parent or another adult. Additionally, abused children displayed increased N2 amplitudes when presented with angry distracter cues, suggesting they expend greater effort inhibiting the involuntary processing of task-irrelevant anger. These ERP data suggest that abused children, when compared with control children, exert more cognitive effort both to engage their attention toward salient anger cues and also to withhold further processing of irrelevant but salient affective cues in the environment.

Physiological Mechanisms Respond to Emotional Input

In a typical social environment, caregivers learn how to recognize and respond to their infants' needs, thereby creating predictable contingencies in the environment. These regularities, in turn, make the infants' environments conducive to further learning. Another way to address issues of learning in emotional development is to examine the extent to which the neurobiological systems that regulate behaviors such as attachment depend on the social experiences afforded to most infants. With this goal, we studied a sample of children who did not receive the kind of emotionally responsive caregiving typically afforded human infants. These children were reared in institutionalized (i.e., orphanage) settings, where a prominent lack of emotional and physical contact from caregivers is a consistent adverse feature of the environment. The specific systems that we explored were the oxytocin and arginine vasopressin (AVP) neurohypophyseal peptide systems. Oxytocin receptors are part of the neural system of reward circuitry that includes the nucleus accumbens. A critical feature of this system for infant development is that it likely confers a sense of security and protection that makes social interactions rewarding. Functionally, central AVP appears to be critical for recognizing familiar individuals, a key component of forming social bonds (Lukas, Bredewold, Landgrave, Neumann, & Veenema, 2011). A growing body of research with rodents suggested that early social experience, through changes in corticotrophin-releasing-hormone (CRH), may alter oxytocin and AVP receptor binding (Champagne, Diorio, Sharma, & Meaney, 2001). Therefore, we reasoned that early social experience would influence the feedback loops involving social reward circuitry, with developmental implications for stress reactivity and behavioral regulation as the infant matures. Indeed, higher levels of oxytocin are associated with decreases in stress (Heinrichs, Baumgartner, Kirschbaum, & Ehler, 2003). We found that children who had experienced early institutional neglect had lower overall levels of AVP than family reared children (Wisner Fries & Pollak, 2004). These results suggest that social deprivation may inhibit the development of the AVP system. Because emotions are inherently regulatory processes, we

evaluated how these neuropeptide systems responded to dynamic social interactions. To do so, we examined hormone levels approximately 20 min after children interacted physically with their mothers. Oxytocin levels for family reared children increased following this interaction. Children who experienced early institutional neglect did not show this response following physical interaction with their adoptive mothers (Wisner Fries et al., 2005). These results suggest that a failure to receive species-typical care disrupts the normal development of the oxytocin and AVP systems in young children. Perturbations in this system may interfere with the calming and comforting effects that typically emerge between young children and familiar adults who provide care and protection.

CAVEATS ABOUT INTERPRETING STUDIES OF MALTREATED CHILDREN

Important basic science issues in emotion are drawn from studies of nonhuman animals in that invasive methods and experimental manipulations that are not possible or appropriate with humans can be used. At the same time, generalizations about the biological processes underlying emotional behaviors across species require caution for a number of reasons (for full discussion of these issues see Sanchez & Pollak, 2009). Animal models do not fully mimic human emotional disorders; brain development, structure, and function are not identical across species; there are chromosomal differences between species; and the actual behaviors exhibited by parents and the way they are received and experienced by offspring are not identical across species. Cross-species comparisons are justified, however, because there may well be common denominators in the roots of emotional functioning across species. One of these may be the role of caregiving, with the effects of poor or inadequate parental nurturance providing critical clues about the mechanisms through which sensory experiences influence emotional development. Indeed, the developmental outcomes of infant maltreatment among nonhuman primates are strikingly similar to those reported in maltreated children (Sanchez et al., 2007).

Most children develop in relatively typical caregiving environments making it difficult to fully evaluate the role of early experiences in the configuration of emotion systems. For this reason, the study of maltreated children may be particularly informative. At the same time, studies of clinical or atypical populations cannot harness the staple tool of experimental psychology: random assignment. One caution about using a phenomenon such as child abuse as a way to understand learning mechanisms underlying emotion is the assumption that abuse is the cause, rather than the correlate, of atypical behavior. Yet converging behavioral genetic data from monkeys and humans highlight the role of postnatal sensory experience in this regard (Jaffee, Caspi, Moffitt, & Taylor, 2004). Behavioral and molecular genetic analyses also support the view that the experience of abuse has a causal role in the formation of emotional behaviors (Kim-Cohen, 2007). Thus, the phenomenon of child maltreatment is well poised to figure prominently in considerations of the relative contributions of learning in emotional development.

IMPLICATIONS FOR PARENTING

What is “Optimal” Parenting?

Primate studies suggest that response-contingent social stimulation (typically first received via the primary caregiver in both humans and nonhuman primates) is a key aspect of the early caregiving environment that plays an important role in organizing the processes responsible for perceiving, interpreting, and responding to social cues. In humans, early infant-caregiver interactions involve highly repetitive, predictable, contingent, and mutually reinforcing sequences, and the infant-caregiver patterns of interactions are probably more predictable than any other sequence experienced by the infant. Our speculation is that high-risk early environments for children are those in which there is a profound lack of socio-

emotional contingencies and reciprocal interactions with caregivers which are necessary to provide a foundation for acquiring expertise in processing socioemotional signals. This suggests that the optimal socioemotional environment is one in which there is regularity, predictability, and contingent responding to the infant. An important caveat here is that humans are likely to be extremely flexible in terms of what constitutes a “good enough” environment. It would be highly maladaptive for humans to require a constrained range of expected social input from caregivers. In the studies that we have conducted with maltreated children, we targeted populations of children who clearly had experiences that were outside of the range of species-expected experiences. We believe the threshold for what constitutes “good” parenting is extremely flexible and broad.

Translation To Practice, Intervention, or Policy

Translational research efforts aimed at understanding the emergence of emotion can meaningfully inform child-oriented interventions for at-risk families. Such research might be aimed at specifying the nature of the emotional input children receive and the mechanisms children use to learn from and respond to their emotional experiences. This type of research would uncover the neurobiological, sensory, and cognitive effects of early experience and thereby help to focus research attention on the precise nature of the problems experienced by children who are at risk for mental health problems. To illustrate, consider one of the common concerns that mental health professionals frequently observe in children who have endured child abuse and/or neglect: subjective feelings of anxiety, fear, or threat. These feeling states may lead children to any number of developmental pathways. Heightened fear might precipitate mood-regulation problems such as anxiety or depression, somatic and general problems with physical health including immune deficiencies, aggressive responses to perceived feelings of threat or insecurity, or perhaps subclinical feelings of unhappiness that detract from a sense of well-being.

One hypothesized pathway through which children's early experiences might impact sensory thresholds for responding to emotional stimuli may be altered perceptual or attentional processing of emotion (e.g., hypersensitivity to threat-related cues, hyposensitivity to positive or security-related cues). Another pathway might involve the L-HPA system, with regulatory peptides (such as corticotropin-releasing hormone, CRH, cortisol) influencing the reciprocal regulatory relation between the frontal cortex and the amygdala. A third potential pathway could involve functioning of the oxytocin system, which could influence children's developing abilities to feel secure, comforted, and protected. The general point is that children may remain responsive to improvements in their early environments. In this manner, interventions aimed at strengthening family systems—with an emphasis on contingent responding—may reduce the mental health burden of those affected by child abuse. Future research that advances our understanding of the specific primary mechanisms affected in individual children could enlighten development of biologically inspired intervention efforts tailored to address specific processes. Some children might benefit from interventions that emphasize a psychoeducational component wherein children receive explicit instruction in learning to read emotional cues, whereas other children might receive experiences that recalibrate perceptual systems of emotional expressions, and still other children might be taught how to test hypotheses about their interpretation of other people's affect. Other kinds of interventions might focus less on perception of sensory input, but promote development of regulatory strategies. Because perceived stress can influence prefrontal functioning through catecholamine-based and CRH-mediated processes, techniques that help children inhibit medial prefrontal activation could help address fearful behaviors. These examples are certainly not meant to be exhaustive. Rather, my intent is merely to speculate about the myriad ways in which advances in basic translational developmental science could spur innovative research into new treatments and how

demonstration of effective ways to treat children with emotion-related difficulties could likewise inform our understanding of the basic mechanisms of emotion.

The historical and technological advances discussed above have led to major advances in understanding biological influences on brain-behavior regulation. For instance, insight into the biological influences of parenting has come from animal model studies showing that rodent maternal behavior can effect long-term changes in responses of the offspring to stress. These changes reflect altered gene expression, so-called “environmental programming” (Meaney & Szyf, 2005). Critical questions remain, such as how to examine the ontogenesis of these mechanisms in humans. Our next steps will be to understand the neurobiological specificity of how these processes operate in humans and then to generate biologically informed interventions to help promote optimal development for all children. A related theme that requires increased attention is deeper understanding of differential sensitivity or vulnerability to environmental effects across individual children. In this regard, animal models of the interactive effects of genes with environmental inputs may highlight these mechanisms.

CONCLUSION

Understanding the processes through which early social experience affects child development increases the likelihood of developing effective prevention and intervention programs. Studying children who have experienced atypical emotion-learning environments, such as maltreated children, also yields valuable knowledge about fundamental issues in psychological science. These include a focus on the neural circuitry and neurobiological regulation of emotion and their subsequent implications for behavior, as well as understanding adaptations and sequelae of chronic social stress exposure on affective neural circuits—especially during periods of rapid neurobiological change when the brain may be particularly sensitive to contextual or environmental influences. We have examined the development of emotion in children whose environments have differed in important ways from a species-typical caregiving environment. The general principle behind these studies is that examining the ways in which aberrant environments influence bio-behavioral development may highlight the nature of the learning mechanisms underlying emotion. Studying this question across species, and across typically and atypically developing populations of children, can highlight learning mechanisms that may not be obvious when emotional development is unfettered. Ongoing research in this area is focusing on defining and specifying ways in which the environment creates long-term effects on brain and behavior, including potential corrective experiences that might foster recovery of competencies and promote health.

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REFERENCES

- Aslin, RN.; Jusczyk, PW.; Pisoni, DB. Speech and auditory processing during infancy: Constraints on and precursors to language.. In: Damon, W.; Kuhn, D.; Siegler, RS., editors. Handbook of child psychology: Vol. 2. Cognition, perception, and language. Wiley; New York: 1998. p. 147-198.
- Bachevalier J, Loveland KA. The orbitofrontal-amygdala circuit and self-regulation of social-emotional behavior in autism. *Neuroscience and Biobehavioral Reviews*. 2006; 30:97–117. [PubMed: 16157377]

- Bauer PM, Hanson JL, Pierson RK, Davidson RJ, Pollak SD. Cerebellar volume and cognitive functioning in children who experienced early deprivation. *Biological Psychiatry*. 2009; 66:1100–1106. [PubMed: 19660739]
- Beale JM, Keil FC. Categorical effects in the perception of faces. *Cognition*. 1995; 57:217–239. [PubMed: 8556842]
- Champagne F, Diorio J, Sharma S, Meaney MJ. Naturally occurring variations in maternal behavior in the rat are associated with differences in estrogen-inducible central oxytocin receptors. *Proceedings of the National Academy of Science, USA*. 2001; 122:12736–12741.
- Darwin, C. *The expression of the emotions in man and animals*. John Murray; London: 1965. (Original work published 1872)
- Giedd JN, Schmitt JE, Neale MC. Structural brain magnetic resonance imaging of pediatric twins. *Human Brain Mapping*. 2007; 28:474–481. [PubMed: 17437295]
- Grippe AJ, Trahanas DM, Zimmerman RR II, Porges SW, Carter CS. Oxytocin protects against negative behavioral and autonomic consequences of long-term social isolation. *Psychoneuroendocrinology*. 2009; 34(10):1542–53. [PubMed: 19553027]
- Hanson JL, Chung MK, Avants BB, Shirtcliff EA, Gee JC, Davidson RJ, Pollak SD. Early stress is associated with alterations in the orbitofrontal cortex: A tensor-based morphometry investigation of brain structure and behavioral risk. *Journal of Neuroscience*. 2010; 60:7466–7472. [PubMed: 20519521]
- Heinricks M, Baumgartner T, Kirschbaum C, Ehlert U. Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. *Biological Psychiatry*. 2003; 1397(54):1389–1398.
- Jaffee SR, Caspi A, Moffitt TE, Taylor A. Physical maltreatment victim to antisocial child: Evidence of an environmentally mediated process. *Journal of Abnormal Psychology*. 2004; 113:44–55. [PubMed: 14992656]
- Kim-Cohen J. Resilience and developmental psychopathology. *Child and Adolescent Psychiatric Clinics of North America*. 2007; 16:271–283. [PubMed: 17349508]
- Lesnik-Oberstein M, Koers AJ, Cohen L. Parental hostility and its sources in psychologically abusive mothers: a test of the three-factor theory. *Child Abuse and Neglect*. 1995; 19:33–49. [PubMed: 7895143]
- Lovic V, Fleming AS. Artificially-reared female rats show reduced prepulse inhibition and deficits in the attentional set shifting task-reversal of effects with maternal-like licking stimulation. *Behavioral Brain Research*. 2004; 148(1-2):209–219.
- Lukas M, Bredewold R, Landgraf R, Neumann ID, Veenema AH. Early life stress impairs social recognition due to a blunted response of vasopressin release within the septum of adult male rats. *Psychoneuroendocrinology*. 2011; 36:843–853. [PubMed: 21185124]
- Meaney MJ, Szyf M. Environmental programming of stress responses through DNA methylation: Life at the interface between a dynamic environment and a fixed genome. *Dialogues In Clinical Neuroscience*. 2005; 7:103–123. [PubMed: 16262207]
- Pollak SD. Early adversity and mechanisms of plasticity: Integrating affective neuroscience with developmental approaches to psychopathology. *Development & Psychopathology*. 2005; 17:735–752. [PubMed: 16262990]
- Pollak SD. Mechanisms linking early experience and the emergence of emotions: Illustrations from the study of maltreated children. *Current Directions in Psychological Science*. 2008; 17:370–375. [PubMed: 21701602]
- Pollak SD, Cicchetti D, Hornung K, Reed A. Recognizing emotion in faces: Developmental effects of child abuse and neglect. *Developmental Psychology*. 2000; 36:679–688. [PubMed: 10976606]
- Pollak SD, Cicchetti D, Klorman R, Brumaghim JT. Cognitive brain event-related potentials and emotion processing in maltreated children. *Child Development*. 1997; 68:773–787.
- Pollak SD, Kistler DJ. Early experience is associated with the development of categorical representations for facial expressions of emotion. *Proceedings of the National Academy of Sciences USA*. 2002; 99:9072–9076.

- Pollak SD, Klorman R, Thatcher JE, Cicchetti D. P3b reflects maltreated children's reactions to facial displays of emotion. *The International Journal of the Society for Psychophysiological Research*. 2001; 38:267–274.
- Pollak SD, Tolley-Schell SA. Selective attention to facial emotion in physically abused children. *Journal of Abnormal Psychology*. 2003; 112:323–338. [PubMed: 12943012]
- Sanchez MM, Alagbe O, Felger JC, Zhang J, Graff AE, Grand AP, Miller AH. Activated p38 MAPK is associated with decreased CSF 5-HIAA and increased maternal rejection during infancy in rhesus monkeys. *Molecular Psychiatry*. 2007; 12:895–897. [PubMed: 17895923]
- Sanchez MM, Noble PM, Lyon CK, Plotsky PM, Davis M, Nemeroff CB, et al. Alterations in diurnal cortisol rhythm and acoustic startle response in nonhuman primates with adverse rearing. *Biological Psychiatry*. 2005; 57:373–381. [PubMed: 15705353]
- Sanchez, MM.; Pollak, SD. Socio-emotional development following early abuse and neglect: Challenges and insights from translational research.. In: de Haan, M.; Gunnar, MR., editors. *Handbook of Developmental Social Neuroscience*. Guilford Press; NY: 2009. p. 497-520.
- Sapolsky RM, Romero LM, Munck AU. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews*. 2000; 21:55–89. [PubMed: 10696570]
- Shackman JE, Shackman AJ, Pollak SD. Physical abuse amplifies attention to threat and increases anxiety in children. *Emotion*. 2007; 7:838–852. [PubMed: 18039053]
- Shackman JE, Fatani S, Camras LA, Berkowitz MJ, Bachorowski J, Pollak SD. Cognition and Emotion. 2010; 24(8):1421–1430.
- Thiessen ED, Hill EA, Saffran JR. Infant-directed speech facilitates word segmentation. *Infancy*. 2005; 7:53–71.
- Wisner Fries AB, Pollak SD. Emotion understanding in postinstitutionalized Eastern European children. *Development and Psychopathology*. 2004; 16:355–369. [PubMed: 15487600]
- Wisner Fries AB, Shirtcliff EA, Pollak SD. Neuroendocrine dysregulation following early social deprivation in children. *Developmental Psychobiology*. 2008; 50:588–599. [PubMed: 18683181]
- Wisner Fries AB, Ziegler TE, Kurian JR, Jacoris S, Pollak SD. Early experience in humans is associated with changes in neuropeptides critical for regulating social behavior. *Proceedings National Academy of Sciences of the USA*. 2005; 102(27):17237–17240.
- Young AW, Rowland D, Calder AJ, Etcoff NL, Seth A, Perret DI. Facial expression megamix: Tests of dimensional and category accounts of emotion recognition. *Cognition*. 1997; 63:271–313. [PubMed: 9265872]