Brain Development in Learning Environments
Embodied and Perceptual Advancements

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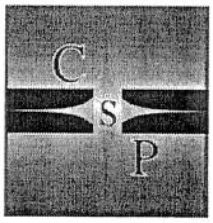

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CHAPTER ONE

A CLOSER LOOK AT THE TRANSACTIONAL NATURE OF EARLY SOCIAL DEVELOPMENT: THE RELATIONS AMONG EARLY CAREGIVING ENVIRONMENTS, TEMPERAMENT, AND EARLY SOCIAL DEVELOPMENT AND THE CASE FOR PHENOTYPIC PLASTICITY

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A rich body of research demonstrates that the quality of the early caregiving environment shapes development. The earliest evidence for the importance of the early caregiving environment comes from studies of maternal deprivation and institutionalization. Sptiz's (1946) description of infants living in foundling and nursery homes showed that institutional care of infants and young children was associated with retardation in physical, motor and intellectual development. Harlow and Suomi (Harlow, 1974; Suomi and Harlow, 1975) found that infant monkeys reared apart from their mothers showed deviant patterns of social behavior with peers. Such evidence inspired Bowlby's ethological theory of attachment (Bowlby, 1969), which suggested that the attachment system serves an adaptive function that promotes survival by ensuring a balance between environmental exploration and proximity to the caregiver. Implicit in Bowlby's theory is the importance of the interaction between the infant and caregiver. It is this interaction that allows the young infant to feel safe and secure in his/her environment, thus providing the freedom to explore and learn about the world.

More recent work indicates that early experiences interact with characteristics of the individual to shape development (Calkins, 2002; Hane, Rubin, Cheah, & Fox, submitted; Pettit & Bates, 1989; Rubin, Burgess and Hastings, 2002), such that suboptimal outcomes are most likely when infant temperamental disposition and caregiver expectations and responsiveness collide to provide a poor fit between organism and environment (Chess &

Thomas, 1991). The present chapter highlights the growing body of literature which elucidates the role of the early caregiving environment and infant temperament in shaping development and the emergent evidence that points to neural mechanisms of influence in the relationship between early experience, child characteristics and developmental outcome. We provide a brief review of the research involving animal and human samples that has examined the effects of early caregiving environments on neurological development. We then turn our attention to the infant's contributions to the quality of early caregiving environments and the evidence derived from behavioral research showing that the temperamental disposition interacts with certain features of the early caregiving environment in shaping social outcome. Finally, we consider the role of phenoplasticity as a potential mechanism by which early caregiving experiences continue to impact development throughout the lifespan.

Early Care Environments and the Developing Brain

In human infants, low degrees of maternal responsiveness to infant cues are associated with lower levels of linguistic functioning (Bornstein and Tamis Le-Monda, 1997) and lower developmental level (Crockenberg, 1983; Olson, Baytes, & Bayles, 1984). Animal studies have revealed similar effects, with low levels of maternal stimulation in the early caregiving context foretelling poor performance on tests of cognition, including spatial and non-spatial learning and memory (Bredy, Humpartzoomian, Cain, & Meaney, 2003; Liu, Diori, Day, Francis, & Meaney, 2000).

Emergent evidence in animal models suggests that the relation between level of maternal stimulation and developmental outcome is a function of the effects of maternal behavior on the developing brain, particularly hippocampal growth (Bredy, Weaver, Champagne, & Meaney, 2001). Studies examining the effects of extreme environmental deprivation in humans and maternal separation in animals provide support for the role of the early caregiving environment in shaping neural development (Francis, Diorio, Plotsky, & Meaney, 2002; Higley et al., 1991; Kuma et al., 2004; Marshall, Fox, and the BEIP Core Group 2004). In the rat, maternal separation during critical periods for brain growth and for periods as brief as a few hours is associated with disrupted hippocampal cytoarchitecture (Kuma et al., 2004). Meaney and his colleagues have shown that even more subtle, naturally occurring variations in quality of maternal caregiving behavior of rat dams shapes the development of the neural substrates that underlie the phenotypic behavioral and endocrine responses to stress in offspring. Compared with adult offspring who received high degrees of maternal licking and grooming and arch-backed nursing in the postnatal period, the adult offspring of dams who provided low degrees of maternal licking and

grooming and arch-backed nursing showed a behavioral response which reflected heightened levels of stress reactivity, including higher frequencies of startle responses, less open-field exploration, and elongated latencies to eat food presented in a novel environment (Caldji et al., 1998; Francis, Diorio, Liu, & Meaney 1999). These differences in behavior were accompanied by corresponding neuroendocrine profiles of heightened fearfulness (Caldji et al., 1998), including decreased central benzodiazepine receptor density in the central, lateral, and basolateral nuclei of the amygdala and locus ceruleus (Caldji et al., 1998); increased plasma adrenocorticotropic hormone and corticosterone responses to restraint stress; and decreased sensitivity to the inhibitory effects of glucocorticoids during conditions of acute stress (Liu et al., 1997).

The effects of early caregiving environments on the neural development of human infants is more difficult to demonstrate given the ethical complications involved in such work. However, one recent study illustrates the plasticity of the developing brain by demonstrating a relation between electrophysiological indices of neurological functioning and extreme environmental deprivation. Marshall, Fox and their colleagues (Marshall, Fox, & the BEIP Core Group 2004) compared electroencephalographic (EEG) power data in multiple frequency bands from a sample of instutionalized infants and young children in Romania to an age-matched control group of Romanian children who were not institutionalized. They found that the instutionalized sample evidenced cortical signs of developmental delay, including higher degrees of low-frequency power in the posterior scalp regions, and decreased high frequency power in the frontal and temporal regions.

Additional research on the effects of early care environments of humans and the developing brain has demonstrated that the environment shapes physiological response to stress vis-à-vis the functioning of the hypothalamic-pituitary-adrenal (L-HPA) system. Flinn and England (1995) showed that children in the rural Caribbean who experienced nonintensive or unstable caretaking had either chronically high cortisol levels or unusually low basal cortisol levels with occasional spikes (Flinn & England, 1995). Duration and severity of child abuse is positively associated with cortisol concentrations in children diagnosed with PTSD (De Bellis et al., 1999). Gunnar, Morison, Chisholm, and Schuder (2001) examined the cortisol levels of children who spent more than 8 months in Romanian orphanages prior to adoption to children who were adopted from Romanian institutions early in infancy and a sample of Canadian born controls and found that the children who had lengthy stays in institutional care showed cortisol levels that were extremely higher than the cortisol levels of found in early adopted and Canadian born groups.

The associations between early caregiving contexts and the L-HPA may be of considerable consequence, as Meaney (2001) has noted that exposure to early

and pronounced stressors which yield dysregulation of the L-HPA axis, predisposes individuals to further problems in dealing with environmental stressors (Meaney, 2001). This persistent difficulty in coping with stress exacerbates risk for behavior and health problems. The neuroendocrine changes associated with dysregulation of the L-HPA axis alter the organism's availability and distribution of energy and increases of cardiovascular tone, which over time may predispose individuals to steroid-induced diabetes, hypertension, and other risk factors for heart disease (Brindley & Rolland, 1989). Other work has shown that degree of L-HPA activation is negatively associated with externalizing, aggressive, or disruptive behavior in children (Tennes & Kreye, 1995; Tout, de Haan, Campbell, & Gunnar, 1998); and is positively associated with internalizing problems, including social withdrawal and anxiety (Ashman, et al., 2002; Kagan, Reznick, & Snidman, 1988; Gunnar, Tout, de Haan, Pierce, & Stansbury, 1997; Schmidt, Fox, Rubin, Sternberg, Gold, Smith, & Schulkin, 1997).

Meaney (2001) has suggested that the relations between individual differences in reactivity to stress and illness may be mediated by parental factors, in particular the naturally occurring differences in maternal care behavior as described in the aforementioned studies of maternal behavior in rats. In our own research we have found support for this notion. In a recent report, we sought to extend the work of Meaney and his colleagues to human infants by measuring the quality of maternal caregiving behavior (MCB) during routine activities such as feeding and changing and then comparing infants who received low quality MCB to those who experienced low quality MCB on indices of stress reactivity also assessed at age 9-months (Hane & Fox, 2006). We found that 9-month-old infants who experienced low quality maternal caregiving behavior (MCB) displayed significantly more fearfulness during the presentation of novel stimuli and less sociability with an experimenter. The infants receiving low quality MCB also showed a pattern of right frontal EEG asymmetry, which is associated with elevated levels of withdrawal motivation (Sutton & Davidson, 1997).

These findings provide the first evidence to support the notion that quality of maternal caregiving in a typically developing human infant sample, i.e., not extreme instances of maternal deprivation, shape neurological development. The infants in the Hane & Fox (2006) sample represent a middle-class, low-risk demographic group, and the measure of MCB, which assessed degree of maternal sensitivity and intrusiveness, captured typical variations in MCB collected from a low-risk sample of mothers and infants—not extreme instances of deprivation, abuse, or neglect. Importantly, infants who received low quality MCB were also more likely to express higher levels of negative affect during

interactions with their mothers than infants in the high quality MCB group, suggesting that the infants' negativity may have influenced the quality of mother-infant interactions. Indeed, a growing body of evidence is revealing the evocative effects of infants in shaping the quality of their own caregiving contexts.

Infant Contributions to Early Care Environments

An important segment of the caregiving literature focuses on the role that the infant brings to the interaction. Our research program has focused on the development of children who manifest strong biases toward approach or withdrawal from novelty. We are interested in two distinct temperamental types of children who are characterized based on their extreme patterns of reactivity to novelty in infancy. The two types of infants differ both in the emotions that they express in response to novelty (one displaying distress and negative affect, the other displaying positive affect), as well as the display of high degrees of motor arousal (common to both). We have followed both groups of infants through middle childhood, examining both behavioral and electrophysiological indices of social and cognitive behavior. The children who expressed negative response to novelty in infancy display behavioral inhibition as toddlers and older children (Calkins & Schmidt, 1995; Fox, Rubin, Calkins, Marshall, Coplan, Porges, Long, & Stewart, 1995) while the children who expressed positive affect to novelty as infants display exuberant affect and social competence. The behaviorally inhibited children are at increased risk for peer rejection and poor social competence in early childhood (Rubin, Chen, & Hymel, 1993; Schmidt, Fox, Schulkin, & Gold, 1999).

There is evidence to suggest that these two groups of children have distinct biological profiles. Behaviorally inhibited infants and young children are more likely to display a pattern of right frontal EEG asymmetry (Fox, Calkins, & Bell, 1994), and the interaction of this asymmetry and their temperament is the best predictor of social reticence at four years of age (Fox, Henderson, Rubin, Calkins, & Schmidt., 2001). Children with right frontal asymmetry are more likely to be behaviorally inhibited and to show difficulty with social interactions (e.g., Fox et al., 1995; 2001). Infants with an exuberant temperament are more likely to display consistently high levels of sociability in the first four years of life when they show a corresponding pattern of left frontal EEG asymmetry (Fox et al., 2001), which may place them at increased risk for the development of externalizing behavior problems (Fox, Schmidt, Calkins, Rubin, & Coplan, 1996).

The aforementioned Hane and Fox (2006) report showed that the quality of early maternal caregiving influenced patterns of frontal EEG asymmetry and behavioral indicators of negative reactivity to yield a profile that is remarkably similar to the description of behaviorally inhibited children. However, importantly, the infants who received low quality MCB in Hane and Fox (2006) were not more likely to be negatively reactive at age 4 months, suggesting that earlier temperament did not influence the effect of MCB on stress reactivity. But, the concurrent temperamental disposition of the infants in the sample was a likely contributor to the effect, as infants who experienced low quality MCB manifested more negative affect while in the care of their mothers. Infant negative affect is likely both a contributor to and a consequence of low quality MCB and, although the challenges in teasing apart the direction of effects are not easily overcome, there is mounting evidence which is elucidating the transactional nature of development by revealing that the quality of the early rearing environments and child temperament act in concert to shape social development.

Transactions between Early Care Environments and Infant Contributions

Evidence from research investigating maternal behavior and temperament indicate that features of the early caregiving environment shape the developing personality. Studies examining the relations between infant and child temperament and maternal behavior indicate that caregiving which is insensitive, or marked by inappropriate or negligible responsiveness to infant signals (Ainsworth, Blehar, & Waters, 1978) is associated with increased negative reactivity to novelty or proneness to distress. Crockenberg and Acredolo (1983) found that infant distress to limitations at 3 months was concurrently related to low degrees of maternal contact with her infant. van den Boom and Hoeksma (1994) found that 6-month-old infants who received caregiving characterized by low frequencies of mother-infant interaction and low degrees of maternal positivity were significantly more likely to be defined as irritable across the first six weeks of the postnatal period than infants receiving more optimal levels of maternal stimulation. Mangelsdorf, Gunnar, Kestenbaum, Lang, & Andreas (1990) found that low levels of maternal sensitive support at infant age nine months were related to higher degrees of infant proneness to distress (Mangelsdorf, et al., 1990). In our own work, we have found that 9-month-old infants reported by their mothers to show low levels of positive affect who also evidenced low degrees of mutual pleasure during play with their mothers showed lower degrees of positive affect during

puppet play with a stranger in the laboratory (Hane, Fox, Polak-Toste, Ghera, and Guner, 2006).

Additional evidence indicates that early individual differences in infant temperament predict variations in insensitive parenting. Ghera, Hane, Malesa, and Fox (2006) found that infants who manifested high degrees of negative reactivity to novelty at age 4 months and who were viewed by their mothers as difficult to soothe were significantly more likely to receive insensitive maternal care in late infancy than infants who manifested low degrees of negative reactivity. Braungart-Rieker and colleagues (Braungart-Rieker, Garwood, & Stifter, 1997) found that 30-month-old children rated by their mothers as highly negatively reactive received less guidance and more controlling behavior from their mothers than their less reactive peers. Taken together, the contemporaneous and predictive relations between temperament and caregiving are indicative of a bi-directional influence, whereby early caregiving may shape the expression of innate temperamental tendencies, and in kind, infant behavior influences maternal behavior throughout infancy and early childhood.

Further evidence indicates that maternal behavior interacts with child temperament in the prediction of childhood behavior problems well into middle childhood. Rubin, Burgess and Hastings (2002) examined the role of parenting in the stability of behavioral inhibition from age two to four and showed that the relation between behavioral inhibition in toddlerhood and reticence at age four was significant and positive for those children who had mothers who were psychologically overcontrolling and derisive. Toddlers who were behaviorally inhibited but who were engaged in mother-child interactions that were controlling or derisive were more likely to be reticent during the preschool years. Rubin, Cheah, and Fox (2001) found that socially reticent behavior in 4-year-olds was associated with maternal behavior that was overly warm and highly controlling during an unstructured free play paradigm. Hane Rubin, Cheah, & Fox (submitted) showed that social withdrawal in middle childhood was predicted by the joint effects of social withdrawal in early childhood and maternal negativity in middle childhood.

Although such evidence suggests that negative maternal behavior contributes to and/or exacerbates problematic behavior, it is imperative to note that temperament alone does not lead to problem behavior, particularly not when the environment is supportive. Indeed, there is ample evidence of developmental resiliency in the temperament literature, as there is evidence to suggest that positive and supportive maternal behavior buffers poor social outcome for temperamentally negative children (Calkins, 2002; Hane et al., submitted; Pettit & Bates, 1989). Calkins (2002) showed that distress to

frustration in toddlerhood was discontinuous across ages 18 to 24 months for children whose mothers engaged them with positively controlling and reinforcing behavior. Pettit and Bates (1989) found childhood aggression was predicted by maternal perceptions of temperamental difficultness and low degrees of proactive maternal involvement; while no relation between temperamental difficulty and aggression emerged for children who experienced high degrees of proactive maternal involvement. Rubin, Cheah and Fox (2001) found that socially reticent behavior at age 4 was predicted by the joint influence of emotion dysregulation and the lack of maternal guidance and control during a teaching task. Emotionally dysregulated children whose mothers provided little guidance and positive control during a structured task were more likely to be reticent during play with unfamiliar age-mates. No such relation between emotion dysregulation and social reticence was yielded for children whose mothers engaged them with positive support and guidance. In a follow-up study of the same children, we found no significant relation between temperamental shyness in early childhood and social withdrawal at age 7 when mothers engaged their children with high degrees of positivity. Temperamentally shy children who experienced maternal behavior characterized by low degrees of positivity were significantly more likely to manifest socially withdrawn behavior than their non-temperamentally shy counterparts (Hane et al., submitted).

The effects of environment may not be limited to maternal behavior, as additional research indicates that other contextual factors, such as early and consistent exposure to peers in nonmaternal childcare settings, is associated with improved outcome for behaviorally inhibited children (Fox et al., 2001). Dettling, Gunnar, and Donzella (1999) revealed that cortisol levels in preschool children enrolled in full-day childcare centers rose steadily during the day, a pattern markedly discrepant from the typical circadian deceleration in cortisol seen in other studies of preschool-aged children. This study also revealed positive relations between increase in cortisol across the day and temperamental shyness in boys and aggression and poor self control in all children. In a more recent study, Watamura, Donzella, Alwin and Gunnar, (2004) showed that insecurely attached children produced higher cortisol levels upon separation with their mothers than their securely attached peers upon beginning first-time enrollment in full-time center-based childcare. Hence, the effects of early caregiving on development are not likely limited to quality of parental care and are certainly not exclusive to features of the maternal caregiving environment. Reliance upon childcare centers and other forms of nonparental care is a growing trend in industrialized nations. As such, careful consideration of the features of these environments that serve to either buffer children from, or

propel them towards, dysregualtion in managing environmental stressors and emotional response to such stressors are as important as the research examining the quality of parental caregiving.

Phenotypic Plasticity and Altered Exteriors

It is our contention that behavioral change is the result of a complex series of transactions between genetic programs that direct the formation and connectivity of brain structures and environmental modifiers of these codes (Fox, Calkins & Bell, 1994). An emergent body of literature supports this notion, as the dynamic neural substrates involved in person-environment transactions are becoming identified in an exciting genre of research studies we have reported herein. Developmental science is working toward understanding the transactional nature of development by designing studies which examine bi-directional relations between the environment and individual differences in the phenotypic expression of responsiveness to the environment. But there is much to be learned about altered phenotypes. Ethologists have documented that environmental factors influence the ability to be influenced by one's environment, or the degree of phenotypic flexibility or plasticity. An interesting illustration comes from a study of phenotypic plasticity in the intertidal snail. Trussell (1996) documented that intertidal snails show morphological changes to the density of their shells upon experimental exposure to predatory crabs. He also showed that a subgroup of snails at greatest environmental risk for predation in the natural habitat from which they were collected, showed the most pronounced degree of exterior predation-induced phenotypic plasticity. In other words, snails showing the greatest growth in shell density were those who dwelled in wave-exposed tidepools where exposure to predatory crabs was high. The case of the intertidal crab is illustrative of the critical role of environmental risk in altering the organism's *proneness* to change. Certain features of the early caregiving environment may not only yield phenotypic changes to the systems involved in regulation of stress, but also to the organism's future propensity to manifest similar phenotypic changes in the future.

We have cited evidence drawn from animal and human studies which demonstrate that early caregiving shapes individual differences in responding to the environment and the physiological systems associated with those behavioral changes (Caldji, et al., 1998; Dettling et al., 1999; Flinn & England, 1995; Francis, Diorio, Liu, & Meaney 1999; Gunnar et al., 2001; Kuma et al., 2004; Watamura et al., 2004), and that contextual factors continue to interact with temperamental differences in the prediction of behavioral and health outcome across development (Calkins, 2002; Hane, Rubin, Cheah, & Fox, submitted; Pettit & Bates, 1989; Rubin, Burgess and Hastings, 2002). Indeed, such

evidence indicates that children are at-risk for poor social outcome only when they manifest an extreme temperamental style and only under certain conditions, such as when they experience parenting marked by high degrees of negativity or low degrees of positivity. Children who experience environmental deprivation, maternal separation, or insensitive parenting may be at continued risk for manifesting phenotypic changes associated with aversive early experience, including dysregulation of the L-HPA axis, a neurological profile consistent with a withdrawal bias and corresponding behavioral signs of social withdrawal and reactivity to stress, because early adversity has primed their systems for such change. Future work which examines the role of phenotypic plasticity in children who have and have not experienced prolonged adversity in the early rearing environment should yield great strides in understanding the sources of risk and resilience in early development.

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