Research Article

Ordinary Variations in Maternal Caregiving Influence Human Infants' Stress Reactivity

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ABSTRACT—We sought to extend earlier work by examining whether there are ordinary variations in human maternal caregiving behavior (MCB) that are related to stress reactivity in infants. We observed 185 mother-infant dyads and used standard coding systems to identify variations in caregiving behavior. We then created two extreme groups and found that infants receiving low-quality MCB showed more fearfulness, less positive joint attention, and greater right frontal electroencephalographic asymmetry than infants receiving high-quality MCB. Group differences in stress reactivity were not a result of measured infant temperament. However, infants receiving low-quality MCB manifested significantly more negative affect during caregiving activities than did infants receiving high-quality MCB. The results suggest that ordinary variations in MCB may influence the expression of neural systems involved in stress reactivity in human infants.

Meaney and his colleagues have observed that in laboratory rats, variations in the maternal caregiving behaviors (MCBs) of archbacked nursing and licking and grooming are stable across multiple litters (Champagne, Francis, Mar, & Meaney, 2003) and influence the development of the neural substrates that underlie the phenotypic behavioral and endocrine responses to stress in offspring (Caldji et al., 1998; Francis & Diorio, 1999; Liu et al., 1997). 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 mothers who provided low degrees of maternal licking and grooming and arch-backed nursing showed a set of outcomes reflecting heightened stress reactivity, including less open-field exploration and elongated latencies to eat food presented in a novel environment (Caldji et al., 1998; Francis & Diorio, 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).

Pruessner, Champagne, Meaney, and Dagher (2004) found that human adults who reported extremely low-quality relationships with their parents evidenced significantly more release of dopamine in the ventral striatum (as evidenced by reduction in [¹¹C]raclopride binding potential) during a stressful event than individuals who reported extremely high-quality relationships with their parents. Research examining the quality of the mother-infant relationship and stress reactivity has documented that a disorganized attachment system is associated with higher concentrations of salivary cortisol (Hertsgaard, Gunnar, Erickson, & Nachmias, 1995). Such evidence suggests that early human caregiving may similarly affect the development of the systems that underlie stress reactivity. We sought to provide support for this claim by examining relations between variations in MCB of human infants and behavioral and physiological markers of stress reactivity. We also considered the role of infant temperament, measured at 4 months of age, in predicting behavioral and physiological markers of stress reactivity.

In human infants, reactivity to stress and novelty has been associated with a pattern of right frontal electroencephalographic (EEG) asymmetry (Fox, Henderson, Rubin, Calkins, & Schmidt, 2001). The pattern of frontal EEG asymmetry may be an important marker of an infant's or child's disposition, or bias, toward withdrawal behaviors. The most consistent data on the relation between right frontal EEG asymmetry and the

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development of social behavior have been found in the literature on the temperament of behavioral inhibition (Davidson, 1994; Fox et al., 1995, 2001; McManis, Kagan, Snidman, & Woodward, 2002). Although the precise origins of this pattern of asymmetry remain unknown, recent work by Davidson (2000, 2004) has suggested that the pattern of frontal asymmetry may reflect unilateral activity in the amygdala. We surmised that variations in maternal behavior during routine caregiving activities, including meal preparation, feeding, and changing of clothing, might be associated with human infants' individual differences in the pattern of frontal EEG asymmetry and corresponding indicators of stress reactivity, including fear responses to novelty and low sociability. In an effort to extend the work of Meaney and his colleagues to human infants, we created two groups of infants based on the quality of their mothers' MCB and compared these groups of infants on frontal EEG asymmetry, fearfulness, and sociability at age 9 months. We predicted that infants who experienced low-quality MCB would exhibit a pattern of right frontal EEG asymmetry and show significantly higher degrees of fearfulness and less sociability than infants who experienced high-quality MCB.

Stress reactivity in infancy may also be a result of an infant's temperament (Fox, Calkins, & Bell, 1994; Fox et al., 2001). A number of researchers have described individual differences in infants' reactions to novelty, with some negatively reactive infants displaying heightened distress and arousal. These infants are perceived as distress-prone by their parents and are likely to display heightened behavioral inhibition to social and nonsocial stimuli as toddlers and preschoolers (Fox et al., 2001). Mothers of negatively reactive infants may be more insensitive in their caregiving responses than other mothers are, as infant negativity is contemporaneously associated with (Mangelsdorf, Gunnar, Kestenbaum, Lang, & Andreas, 1990; van den Boom & Hoeksma, 1994) and predictive of (Braungart-Rieker, Garwood, & Stifter, 1997; Crockenberg & Smith, 1982; Ghera, Hane, Malesa, & Fox, 2006) suboptimal levels of maternal sensitivity. We thus examined infant temperament as a potential contributor to stress reactivity differences in our caregiving groups. Specifically, we examined the role of reactivity to novelty at age 4 months as a predictor of frontal EEG asymmetry, fearfulness, and sociability at age 9 months. And, to elucidate the infants' contributions to the caregiving environment at age 9 months, we evaluated the degree to which infants in the high- and low-quality MCB groups differed on level of negative affect expressed during the same caregiving activities in which quality of MCB was rated.

METHOD

Participants

Participants were seen as part of a larger longitudinal investigation exploring the role of temperament in the growth of social competence from ages 4 months to 5 years. As part of this study, 779 infants were screened for emotional and motor reactivity to

month laboratory visit were invited to participate in laboratory and home visits. Of these infants, 61 were randomly chosen to serve as control subjects, 67 were selected on the basis of their high degrees of negative reactivity to novelty, and 57 were selected on the basis of their high degrees of positive reactivity to novelty. The mothers' average age was 32.4 years (SD = 5.4), and all were middle class and at least high school educated. Of the infants, 123 (66.5%) were Caucasian, 22 were African American (11.9%), 16 were of Hispanic origin (8.6%), 2 were Asian American (1.1%), and 22 were of other or mixed ethnicity (11.9%). ed CB

4-Month Assessment: Reactions to Novelty and Creation of Temperament Groups

novelty at age 4 months (e.g., see Fox et al., 2001). At age 9

months, 185 infants (100 female) who participated in the 4-

During a laboratory visit at age 4 months, infants were presented with two sets of brightly colored mobiles varying in the number of dangling toys and with two sets of auditory stimuli (see Calkins, Fox, & Marshall, 1996; Fox et al., 2001). The infants' behavior during this reactivity paradigm was videotaped and subsequently coded for degree of negative affect, positive affect, and gross motor arousal. Degree of negative reactivity was assessed using the Negative Affect Scale, which rates the intensity of negative affect as indexed by levels of fussing, fretting, and crying. Positive reactivity was rated with the Positive Affect Scale, which gauges the degree of smiling and neutral or positive vocalizations, and motor movement was measured by intensity and duration of arm and leg movements (Calkins et al., 1996; Fox et al., 2001).

Of the 779 infants screened at age 4 months, the first 100 infants, regardless of temperament, were invited to participate in the remainder of the study to serve as a random control group. The infants in the control group were rated for degree of positive, negative, and motor reactivity and were used to set the selection criteria for all subsequent infants. Infants who scored above the control group's mean on negative affect and motor activity and below the control group's mean on positive affect were invited to participate in the remainder of the study to serve as the negatively reactive group. Infants who scored above the mean on positive affect and motor activity and below the mean on negative reactivity were included in the positively reactive group.

9-Month Assessment

During the 9-month laboratory visit, EEG data were collected, and infants underwent the Laboratory Temperament Assessment Battery (Lab-TAB; Goldsmith & Rothbart, 1999). The Early Social Communication Scales (ESCS; Mundy et al., 2003) were also administered by a trained examiner.

Within 2 weeks of the laboratory visit, mother and infant were scheduled for a home visit. During this visit, they were video-

taped as they interacted in a series of object-focused and routine caregiving contexts, including the mother being busy in the kitchen (8 min), snack time (i.e., spoon-feeding of solids; 5 min), and caregiving and changing activities (i.e., change of clothing and application of lotion; 5 min).

Quality of MCB

The mothers' behavior during the home visit was video-recorded and subsequently rated for degree of sensitivity (Ainsworth, 1976) and intrusiveness (Park, Belsky, & Putnam, 1997). Maternal sensitivity was determined using a modified version of Ainsworth's (1976) system for rating MCB. Of Ainsworth's original 28 scales, the following 9-point rating scales were used: Acceptance-Rejection, Sensitivity-Insensitivity, Degree of Availability, and Appropriateness of Pace in Feeding. Maternal intrusiveness was rated globally using the 4-point scale of Park et al. (1997) and Ainsworth's Cooperation-Interferences scale (reverse-scored); these ratings were then averaged, such that higher scores indicated more maternal intrusiveness. To ensure that the measure of MCB was not confounded by intrusive maternal behavior, we subtracted the intrusiveness composite for each episode (i.e., mother busy in the kitchen, snack time, caregiving and changing) from the sensitivity composite for that episode. A final MCB composite was derived by averaging these episode aggregates, such that higher scores indicated higher quality of MCB, or maternal behavior that was both sensitive and nonintrusive. Two independent raters achieved sound interrater reliability across 40 cases, with intraclass rs in each interactive episode ranging from .59 to .84, an overall sensitivity reliability coefficient of .80, and an overall intrusiveness reliability coefficient of .76. The composite measure of MCB was normally distributed (see Fig. 1).

Quality of Infant Affect During Mother-Infant Interaction

Kochanska's (1997, 1998) scales for rating the affective quality of mother-infant interaction were used to assess the degree of the infants' negative affect during the home-based interactions. The quality of maternal and infant affect was rated separately in 30-s segments. Each 30-s segment was coded for multiple discrete infant affects: tenderness-affection (hugging, kissing), joy (smiling, laughing), and *discrete negativity* (frowning, fussing, or crying). Or, in the absence of a single discrete event in a given 30-s segment, one general mood code (positive or negative) was assigned. A negative mood code was assigned if the infant manifested signs of distress, fear, fatigue, or disinterest, and a positive mood code was assigned if the infant was pleasant or content and appeared to be interested in the ongoing activity. A negative affect score was derived by summing the number of segments in which either discrete negativity or negative mood was present and then dividing this sum by the total number of coded segments. A positive affect score was obtained by summing the number of segments in which either discrete negativity or negative mood was present and dividing this sum by the total

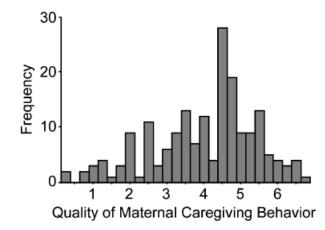


Fig. 1. Frequency distribution of the quality of maternal caregiving behavior.

number of coded segments. For each of the three interactive episodes (mother busy in the kitchen, snack, and caregivingchanging), positive- and negative-affect scores were derived. A *routine caregiving composite* was obtained by averaging these two scores across the interactive episodes.

Two independent raters who were blind to all data on the infants' temperament coded affect in the videotapes taken during the home visits. These raters achieved sound interrater reliability (average kappa value of .78).

Frontal EEG Asymmetry

During the 9-month laboratory visit, EEG was acquired for each infant. Infants were seated in their mothers' laps as a metal bingo wheel was placed on a table in front of them. An experimenter placed one, three, or seven brightly colored balls in the wheel and spun it for six 20-s trials that were separated by 10-s intervals. The infants were fitted with a Lycra stretch cap containing electrodes corresponding to the 10-20 system of electrode placement. The cap was secured by a headband and by two straps on either side that were connected to a vest worn by the infant. Prior to collection, each of the 12 active sites of collection (F3, F4, F7, F8, Fz, P3, P4, Pz, O1, O2, T7, and T8) and the reference site (Cz) were abraded and prepped appropriately.

Two Beckman mini-electrodes (one placed at the supra orbit and the other at the outer canthus) were used to record one channel of electro-oculogram (EOG) from the left eye. EEG and EOG data were amplified with a high-pass setting of 0.1 Hz and a low-pass setting of 100 Hz on custom bio-amplifiers made by SA Instrumentation (Encinitas, CA). The EEG data were digitized at a rate of 512 Hz throughout acquisition and rereferenced using the average reference configuration. The digitized data were displayed graphically for artifact scoring, and portions of EEG marked by movement artifact were removed from all channels of the EEG record prior to further analysis. Blinks were regressed out of portions of EEG that were clearly marked with eye movement.

The rereferenced, artifact-scored EEG data were analyzed with discrete Fourier transform analysis, and power in picowatt ohms (or microvolts squared) was computed for each channel. Spectral power data in single-hertz frequency bins from 1 through 30 Hz were computed for each of the trials at each of the collection sites. For each collection site, power in the 6- to 9-Hz frequency band was computed by summing the power in the single-hertz bins for these four frequencies across trials. It has been suggested that in 9-month-olds, the 6- to 9-Hz band reflects alpha-like activity (Marshall, Bar-Haim, & Fox, 2002).

We used log power data from the frontal and parietal regions (F3 and F4, P3 and P4) to calculate the asymmetry index. Asymmetry was computed as power in the right lead minus power in the left lead for homologous leads (for both frontal and parietal leads). Inasmuch as activation and power in the alpha band are reciprocally related (Davidson, 1988), negative asymmetry scores represent right asymmetry, and positive scores represent left asymmetry.

Infant Fearful Response

During the 9-month laboratory visit, the infants underwent the masks paradigm of the Lab-TAB (Goldsmith & Rothbart, 1999), which is designed to elicit fearful behavior. The infants were seated in a high chair with a table directly in front of them. A large cardboard screen with a door was placed on the table. Two masks, one of an old man and another of a clown, were presented once each through this door. Each mask was presented for 10 s. *Fearful response* was scored by averaging the ratings for startle (presence/absence), self-stimulation (presence/absence), intensity of bodily fear (0-3), and intensity of escape (0-3) and subtracting from this average the mean of intensity of positive facial expression (0-3) and positive motor arousal (presence/ absence). A higher score indicates more fearfulness. Interrater reliability for each of the scales entering into the fearful composite was achieved by two independent observers who were blind to all other data in the study (kappas ranged from .65 to 1.0).

Infant Social Behavior

To index the infants' social behavior, we administered the ESCS (Mundy et al., 2003) during the 9-month laboratory visit. The ESCS is a structured assessment involving the presentation of a series of seven mechanical and windup toys by a trained experimenter. The toys are presented in a series of 21 trials while the infant is seated on his or her mother's lap. A score for initiating joint attention (IJA) is derived from this measure and describes the raw number of times the infant alternates eye contact between the active mechanical toys and the tester, points to the toys, or shows the toys in order to share the experience with the tester. For this study, we used scores for *positive IJA*, the proportion of trials in which the infant initiated joint

attention in an affectively positive manner. Positive IJA is thought to be an index of infants' positive sociability, inasmuch as it represents pleasure in sharing a common experience with an unfamiliar adult. Two coders independently rated 25 cases and achieved sound interrater agreement (positive IJA $\alpha = .90$).

RESULTS

Preliminary Analyses

Table 1 provides descriptive statistics for each key measure across the entire sample. No significant sex differences were found for any of the key variables in this study.

Creation of Caregiving Groups

Two groups of infants were created on the basis of the quality of MCB. Infants whose mothers scored more than 1 standard deviation above the sample mean for the normally distributed MCB composite (see Fig. 1) were placed in the high-quality MCB group (n = 25), and infants whose mothers scored more than 1 standard deviation below the sample mean were placed in the low-quality MCB group (n = 34). Because the sample included both randomly selected and temperamentally extreme children, we examined the degree to which placement into the two caregiving groups varied as a function of infants' sex and temperament group (control, positively reactive, and negatively reactive). Both analyses yielded nonsignificant chi-square statistics. Table 2 depicts the distribution of infants in each MCB group across the three temperament groups.

Maternal Caregiving and Stress Reactivity

We computed three one-way univariate analyses of variance (ANOVAs) to determine whether frontal EEG asymmetry, fearfulness, and sociability differed between infants who experienced low-quality MCB with those who experienced highquality MCB. Compared with infants in the high-quality MCB group, those in the low-quality MCB group were significantly more likely to exhibit a pattern of right frontal EEG asymmetry, F(1, 41) = 5.28, $p_{rep} = .98$, $\eta^2 = .11$, and exhibited significantly more fearfulness, F(1, 51) = 3.94, $p_{rep} = .97$, $\eta^2 = .07$. They were also significantly less likely to manifest positive IJA,

TABLE 1

Summary of Infant Measures Obtained at Age 9 Months

| Variable | n | М | SD |
|---|-----|------|------|
| Quality of maternal caregiving behavior | 185 | 4.00 | 1.40 |
| Frontal electroencephalogram asymmetry | 144 | .01 | .28 |
| Fearful response | 159 | 02 | .88 |
| Positive joint attention | 176 | .22 | .25 |
| Infant negative affect | 176 | .64 | .54 |
| Infant positive affect | 175 | .62 | .48 |

TABLE 2

| Number of Infants in Each Maternal-Caregiving-Behavior |
|--|
| Group Within Each Temperament Group |

| Temperament group | Maternal-caregiving-behavior group | | |
|---------------------|------------------------------------|--------------|--|
| | Low quality | High quality | |
| Control | 17 | 8 | |
| Positively reactive | 10 | 10 | |
| Negatively reactive | 7 | 7 | |

F(1, 52) = 5.60, $p_{rep} = .99$, $\eta^2 = .10$. A similar analysis of degree of EEG asymmetry in the parietal region yielded no significant main effect of MCB group, F < 1, suggesting that the group difference in EEG asymmetry is specific to the frontal region.

Infant Temperament and Stress Reactivity

To rule out the competing hypothesis that differences in stress reactivity were a function of 4-month temperament group, we computed a series of one-way univariate ANOVAs. Temperament group had no significant main effects on frontal or parietal EEG (6–9 Hz), fearfulness, or sociability.

Infant Negative Affect During Mother-Infant Interaction and MCB

Last, we sought to elucidate infants' contributions to the caregiving environment by evaluating the degree to which infants in the high- and low-quality MCB groups differed on level of negative affect expressed during the same caregiving activities in which quality of MCB was rated. Results of an ANOVA indicated that infants in the low-quality MCB group expressed significantly more negative affect while in the care of their mothers than did infants in the high-quality MCB group, F(1, 54)= 24.42, $p_{\rm rep}$ = .99, η_p^2 = .27. An ANOVA examining degree of positive affect yielded no significant differences between the MCB groups. There were no significant differences for negative or positive affect during caregiving as a function of 4-month temperament group. Figure 2 provides a graphical depiction of all significant mean differences between MCB groups.

DISCUSSION

Meaney and his colleagues showed that naturally occurring variations in MCB of rat dams were associated with behavioral and physiological markers of heightened stress reactivity of their offspring (Caldji et al., 1998; Francis & Diorio, 1999; Liu et al., 1997). Our results are consistent with this research. We found that relative to infants who experienced high-quality MCB, infants who experienced low-quality MCB displayed significantly more fearfulness during the presentation of novel

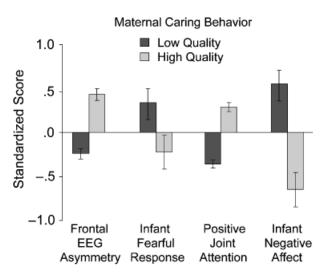


Fig. 2. Mean frontal electroencephalographic (EEG) asymmetry, fearful response, negative affect during mother-infant interaction, and positive joint attention among infants who experienced low-quality and high-quality maternal caregiving behavior. Error bars show standard errors.

stimuli, less positive joint attention to a shared object, and more right frontal asymmetry.

These findings suggest that variations in human maternal caregiving may influence stress reactivity of offspring. These findings join a rich literature indicating that the quality of early caregiving environments shapes behavioral development among both animals and humans (Caldji et al., 1998; Francis & Diorio, 1999; Kuma et al., 2004; Liu et al., 1997; Marshall, Fox, & the BEIP Core Group, 2004; Suomi, Collins, & Harlow, 1973). And they support the work of Meaney and his colleagues (see Meaney, 2001, for a review), who have demonstrated that naturally occurring variations in MCB in the rat are of substantial consequence. The infants in this sample represent a middleclass, low-risk demographic group, and the measure of MCB, which assessed degree of maternal sensitivity and intrusiveness, captures ordinary variations in MCB-not extreme instances of deprivation, abuse, or neglect. Thus, our findings indicate that normal fluctuations in the quality of early care are of substantial developmental relevance, even for low-risk populations.

The pattern of fearfulness, low sociability, and right frontal EEG asymmetry found in the low-quality MCB group has been identified in infants displaying negative reactivity to novelty and behavioral inhibition during the early years of life (Fox et al., 1995, 2001). However, negatively reactive fearful infants were not overrepresented in the low-quality MCB group. Infants in this group did exhibit more negative affect (distress and crying) during routine caregiving in the home, compared with infants in the high-quality MCB group. This finding suggests that the infants' negativity may have influenced the quality of mother-infant interactions. Similar findings have been reported previously in the human developmental literature (Crockenberg & Acredolo, 1983; Mangelsdorf et al., 1990; van den Boom & Hoeksma, 1994).

A growing body of literature indicates that temperament and maternal behavior act in concert to shape development (Calkins, 2002; Hane, Rubin, Cheah, & Fox, 2005; Pettit & Bates, 1989; Rubin, Burgess, & Hastings, 2002). Research examining stress reactivity in particular has shown that temperament interacts with the quality of the mother-infant relationship in predicting stress reactivity, such that toddlers who have a fearful or inhibited disposition and an insecure relationship with their mothers are the most likely to experience elevated salivary cortisol levels (Nachmias, Gunnar, Mangelsdorf, Parritz, & Buss, 1996; Spangler & Schieche, 1998). Given such evidence, it is apparent that the boundary between person and environment in the development of stress reactivity is indistinct. Early caregiving shapes the expression of innate temperamental tendencies by yielding phenotypic changes to the neurological systems that regulate reactivity to stress and novelty. Those changes in stress reactivity may in turn elicit changes in the environment by altering quality of MCB. Certain features of the early caregiving environment may yield contemporaneous phenotypic changes to the systems involved in regulation of stress and also to the organism's future propensity to manifest similar phenotypic changes in the future (Hane & Fox, 2005), a phenomenon documented by evolutionary biologists and referred to as phenotypic plasticity.

Thus, infants who manifest extreme patterns of temperamental reactivity from birth may be more likely than others to elicit insensitive parenting, and insensitivity parenting, in turn, sets in place a pattern of phenotypic changes that both alter the infants' behavior at that time and prime the infants to respond in a similar fashion to similar environmental stressors in the future. Hence, infants who receive low-quality MCB may manifest a resultant heightened level of reactivity to similar stressors in the future (e.g., when presented with challenging interpersonal exchanges in future relationships with parents, peers, or romantic partners). Such heightened stress reactivity may place such individuals at further risk for behavioral and health problems associated with prolonged dysregulated reactions to stress (Meaney, 2001). Long-term investigations of infant and maternal behavior, beginning at birth, should prove most informative in elucidating the complex series of person-by-environment transactions involved in the development of stress reactivity, its neurological concomitants, and long-term behavioral and health sequelae.

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REFERENCES

- Ainsworth, M.D.S. (1976). Technical manual for the Systems for Coding Infant Attachment and Reciprocal Maternal Behaviors. Princeton, NJ: Educational Testing Service.
- Braungart-Rieker, J.M., Garwood, M.M., & Stifter, C.A. (1997). Compliance and noncompliance: The roles of maternal control and child temperament. *Journal of Applied Developmental Psychology*, 18, 411–428.
- Caldji, C., Tannenbaum, B., Sharma, S., Francis, D., Plotsky, P.M., & Meaney, M.J. (1998). Maternal care during infancy regulates the development of neural systems mediating the expression of fearfulness in the rat. *Proceedings of the National Academy of Sciences*, USA, 95, 5335–5340.
- Calkins, S.D. (2002). Does aversive behavior during toddlerhood matter? The effects of difficult temperament on maternal perceptions and behavior. *Infant Mental Health Journal*, 23, 381–402.
- Calkins, S.D., Fox, N.A., & Marshall, T.R. (1996). Behavioral and physiological antecedents of inhibition in infancy. *Child Devel*opment, 67, 523–540.
- Champagne, F.A., Francis, D.D., Mar, A., & Meaney, M. (2003). Variations in maternal care in the rat as a mediating influence for the effects of environment on development. *Physiology and Behavior*, 79, 359–371.
- Crockenberg, S., & Acredolo, C. (1983). Infant temperament ratings: A function of infants, of mothers, or both? *Infant Behavior & De*velopment, 6, 61–72.
- Crockenberg, S.B., & Smith, P. (1982). Antecedents of mother-infant interaction and infant irritability in the first 3 months of life. *Infant Behavior & Development*, 5, 105–119.
- Davidson, R.J. (1988). EEG measures and cerebral asymmetry: Conceptual and methodological issues. *International Journal of Neuroscience*, 39, 71–89.
- Davidson, R.J. (1994). Asymmetric brain function, affective style, and psychopathology: The role of early experience and plasticity. *Development and Psychopathology*, 6, 741–758.
- Davidson, R.J. (2000). Affective style, psychopathology, and resilience: Brain mechanisms and plasticity. *American Psychologist*, 55, 1196–1214.
- Davidson, R.J. (2004). What does the prefrontal cortex "do" in affect: Perspectives on frontal EEG asymmetry research. *Biological Psychiatry*, 67, 219–223.
- Fox, N.A., Calkins, S., & Bell, M.A. (1994). Neural plasticity and development in the first two years of life: Evidence from cognitive and socioemotional domains of research. *Development and Psychopathology*, 6, 677–696.
- Fox, N.A., Henderson, H.A., Rubin, K.H., Calkins, S.D., & Schmidt, L.A. (2001). Continuity and discontinuity of behavioral inhibition and exuberance: Psychophysiological and behavioral influences across the first four years of life. *Child Development*, 72, 1–21.
- Fox, N.A., Rubin, K.H., Calkins, S.D., Marshall, T.R., Coplan, R.J., Porges, S.W., Long, J., & Stewart, S. (1995). Frontal activation asymmetry and social competence at four years of age. *Child Development*, 66, 1770–1784.
- Francis, D.D., & Diorio, J. (1999). Nongenomic transmission across generations of maternal behavior and stress response in the rat. *Science*, 286, 1155–1158.
- Ghera, M.M., Hane, A.A., Malesa, E.E., & Fox, N.A. (2006). The role of infant soothability in the relation between infant negativity and maternal sensitivity. *Infant Behavior & Development*, 29, 289– 293.

- Goldsmith, H.H., & Rothbart, M.K. (1999). The Laboratory Temperament Assessment Battery (version 1.3; locomotor version), Unpublished manuscript, University of Oregon, Eugene.
- Hane, A.A., & Fox, N.A. (2005). 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. Unpublished manuscript, University of Maryland, College Park.
- Hane, A.A., Rubin, K.H., Cheah, C.S.L., & Fox, N.A. (2005). The role of maternal behavior in the relation between shyness and social withdrawal in early childhood and social withdrawal in middle childhood. Manuscript submitted for publication.
- Hertsgaard, L., Gunnar, M., Erickson, M.F., & Nachmias, M. (1995). Adrenocortical responses to the strange situation in infants with disorganized/disoriented attachment relationships. *Child Devel*opment, 66, 1100–1106.
- Kochanska, G. (1997). Multiple pathways to conscience for children with different temperaments: From toddlerhood to age 5. *Devel*opmental Psychology, 33, 228–240.
- Kochanska, G. (1998). Mother-child relationship, child fearfulness, and emerging attachment: A longitudinal study. *Developmental Psychology*, 34, 480–490.
- Kuma, H., Miki, T., Matsumoto, Y., Gu, H., Li, H.P., Kusaka, T., Satriotomo, I., Okamoto, H., Yokoyama, T., Bedi, K.S., Onishi, S., Suwaki, H., & Takeuchi, Y. (2004). Early maternal deprivation induces alterations in brain-derived neurotrophic factor expression in the developing rat hippocampus. *Neuroscience Letters*, 373, 68–73.
- Liu, D., Diorio, J., Tannenbaum, B., Caldji, C., Francis, D., Freedman, A., Sharma, S., Pearson, D., Plotsky, P.M., & Meaney, M.J. (1997). Maternal care, hippocampal glucocorticoid receptors, and hypothalamic-pituitary-adrenal responses to stress. *Science*, 277, 1659–1662.
- Mangelsdorf, S., Gunnar, M., Kestenbaum, R., Lang, S., & Andreas, D. (1990). Infant proneness-to-distress temperament, maternal personality, and mother-infant attachment: Associations and goodness of fit. *Child Development*, 61, 820–831.
- Marshall, P.J., Bar-Haim, Y., & Fox, N.A. (2002). Development of the EEG from 5 months to 4 years of age. *Clinical Neuropsychology*, 113, 1199–1208.
- Marshall, P.J., Fox, N.A., & the BEIP Core Group. (2004). A comparison of the electroencephalogram between institutionalized and community children in Romania. *Journal of Cognitive Neuroscience*, 16, 1327–1338.

- McManis, M.H., Kagan, J., Snidman, N.C., & Woodward, S. (2002). EEG asymmetry, power, and temperament in children. *Developmental Psychobiology*, 41, 169–177.
- Meaney, M.J. (2001). Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. Annual Reviews in Neuroscience, 24, 1161–1192.
- Mundy, P., Delgado, C., Block, J., Venezia, M., Hogan, A., & Seibert, J. (2003). A manual for the abridged Early Social Communication Scales (ESCS). (Available from the Psychology Department, 5665 Ponce de Leon Blvd., #350 FHF Building, University of Miami, Coral Gables, FL 33146)
- Nachmias, M., Gunnar, M., Mangelsdorf, S., Parritz, R.H., & Buss, K. (1996). Behavioral inhibition and stress reactivity: The moderating role of attachment security. *Child Development*, 67, 508–522.
- Park, S., Belsky, J., & Putnam, S. (1997). Infant emotionality, parenting, and 3-year inhibition: Exploring stability and lawful discontinuity in a male sample. *Developmental Psychology*, 33, 218–227.
- Pettit, G.S., & Bates, J.E. (1989). Family interaction patterns and children's behavior problems from infancy to 4 years. *Developmental Psychology*, 25, 413–420.
- Pruessner, J.C., Champagne, F., Meaney, M.J., & Dagher, A. (2004). Dopamine release in response to a psychological stress in humans and its relationship to early maternal care: A positron emission tomography study using [C]raclopride. *Journal of Neuroscience*, 24, 2825–2831.
- Rubin, K.H., Burgess, K.B., & Hastings, P.D. (2002). Stability and social-behavioral consequences of toddlers' inhibited temperament and parenting behaviors. *Child Development*, 73, 483–496.
- Spangler, G., & Schieche, M. (1998). Emotional and adrenocortical responses of infants to the strange situation: The differential function of emotional expression. *International Journal of Beha*vioral Development, 22, 681–706.
- Suomi, S.J., Collins, M.L., & Harlow, H.F. (1973). Effects of permanent separation from mother on infant monkeys. *Developmental Psychology*, 9, 376–384.
- van den Boom, D.C., & Hoeksma, J.B. (1994). The effect of infant irritability on mother-infant interaction: A growth-curve analysis. *Developmental Psychology*, 30, 581–590.

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