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Stability of Parental Care across Siblings from Undisturbed and Challenged Pregnancies: Intrinsic Maternal Dispositions of Female Rhesus Monkeys

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Abstract

The concept of fetal programming is based on the idea that the developmental trajectory of infants is adjusted in response to *in utero* conditions. In species with extended parental care, these prenatally-derived tendencies are further substantiated by behavioral attributes of the mother during the postnatal period. We investigated the stability of maternal behavioral interactions with infant monkeys, and carefully varied prenatal conditions across siblings reared by the same mother. We hypothesized that effects of prenatal disturbance and the infant's susceptibility would be differentially affected by maternal attributes. Hierarchical Linear Modeling was employed to analyze observational data on 121 rhesus macaques reared by a total of 35 multiparous mothers. A portion of the variance in 5 dyadic behaviors was statistically driven by the infant (or was unique to a particular mother-infant pair), but stable maternal propensities and a consistent style of care across siblings also substantially influenced behavioral interactions. Moreover, the magnitude and direction of the prenatal effects were contingent on a female's intrinsic dispositions. When mothers typically exhibited high levels of a corresponding behavior, responsiveness to infants was enhanced as a consequence of prenatal disturbance. The opposite was true for less expressive females. Challenges to the wellbeing of pregnancy thus served to accentuate maternal predispositions and served to magnify the range of variation in mother-infant behavior across the whole population.

Keywords

Mother-Infant Relationships; Prenatal Stress; Hierarchical Linear Modeling; Rhesus Macaque; Maternal Care

Introduction

Because the future is and always has been uncertain, no parent can know for sure what rearing strategy will optimally promote each infant's wellbeing (Ellis, Boyce, Belsky,

Bakermans-Kranenburg & van IJzendoorn, 2011). A degree of behavioral plasticity and responsiveness to environmental context, during both prenatal and postnatal periods, thus culminates in the optimal strategy to ensure offspring survival (Barker 1998; Jones, 2005). Maternal care has the potential to protect and buffer children (Shonkoff, 2010), or mothers can further challenge and add difficulty if they provide neglectful and abusive care (Shirtcliff, Hanson, Rudolph, Strang & Pollak, under review). Empirical research on this topic is often challenging because it is difficult to disentangle the relative contributions of caregiver versus infant attributes (Hrды, 1999; Rosenblum & Lewis, 1974). In addition, parenting may be modified in a contingent manner in response to environmental demands (Bugental & Happaney, 2004, Bugental et al, 2010). The purpose of the present study was two-fold. First, we determined whether a mother's caregiving style was relatively stable across all of her infants. Second, we established how a period of disturbance during pregnancy affected these dyadic interactions. We predicted that behavioral effects of prenatal disturbance would depend in part on a female's disposition toward maternal care.

Is dyadic behavior stable for each mother across all of her infants?

Maternal care ensures infant survival and is needed to promote behavioral development. Some caregiving behaviors are essential and likely to be stable from one infant to the next. For example, female rodents consistently lick and groom pups at high rates, and this parenting style initiates a developmental trajectory in which offspring are emotionally resilient with unique developmental, neurochemical and neuroendocrine phenotypes (Weaver et al., 2004; Uriarte et al., 2007). In monkeys, some mothers serially abuse multiple offspring, generally recapitulating their own early rearing experience (Maestripieri, 2005a, b; Maestripieri et al., 1999). Mantymaa and colleagues (2006a) observed similar continuity such that human mothers' interactive and affective behaviors were similar to what they had received in terms of sensitivity, responsiveness, warmth, and acceptance.

Nevertheless, it is difficult to gauge the intrinsic components of a parent's nurturing style because the familial context changes. Maternal responsiveness will be based on current signals about viability and vigor of each infant, balanced with the resources at her disposal (Schlomer, Del Giudice & Ellis, 2011) and her own potential for future reproduction (Hrды, 1999). In natural conditions and nonindustrialized countries, compensatory responses for a compromised or impaired infant are further moderated by the demands to obtain food, and the abundance or scarcity of ecological resources (Walker et al., 2008). Caregiving can thereby change in a contingent manner with respect to exigent circumstances (Adam, Klimes-Dougan, & Gunnar, 2007; Andrews and Rosenblum, 1988, 1991, 1994). Accordingly, a unique feature of our experimental approach was that husbandry and rearing conditions could be held constant across all infants. Older, weaned siblings were removed so that each mother raised only one infant at the time, while her rearing of several offspring was evaluated.

Are these dyadic interactions affected by prenatal disturbance?

From one infant to the next, mothers make explicit and implicit decisions about how to interact, especially if the new one is disabled, sick, or at-risk (Berkson, 1977, Nakamichi, 1986). This tradeoff is especially salient for high-investment species, as most primates are,

because many months have been invested in gestation by the time of birth, and even more effort will be required to ensure that the offspring's potential is realized (Fisher & Blomberg, 2011; Walker et al., 2008). In parallel, susceptibility of the developing fetus to extrinsic stimuli begins *in utero* and this prenatal responsiveness helps to establish the regulatory set points for many physiological systems (Barker, 1998; Bateson et al., 2004; Gluckman, Hanson, Cooper, & Thornburg, 2008). Developmental trajectories in the offspring may be adjusted to 'make the best of a bad situation' following early insults and environmental perturbations, sometimes even by accelerating the maturation of neural development and autonomous behavior after birth (Jones, 2005). A demanding and stressful prenatal environment may thus send an early warning signal that helps canalize development, strategically preparing the offspring for later adversity.

Human mothers and animals have been observed to display solicitous care for infants with physical disabilities or behavioral problems (Mann, 1992; Davis & Todd, 1999). The additional attention can help buffer the child, culminating in substantial catch-up in their development during the rearing period (Hokken-Koelega et al., 1995; Meaney & Szyf, 2005). Many low birth weight infants eventually show typical cognitive and socio-emotional development in response to high maternal acceptance, stimulation and organized care (Bradley, Whiteside, & Mundform, 1994). Bugental and colleagues (2004, 2010) suggested that the nature of maternal adjustment for a given infant is influenced by the nurturing style that a mother *typically* provides to her offspring as well as other maternal characteristics (Hrdy, 1999). Our analyses were designed to test this hypothesis by comparing the maternal care of female rhesus monkeys across multiple infants, also focusing on dyadic behavior after pregnancies that included a period of stressful disturbance.

Adverse pregnancies in humans are typically embedded in a larger economic and social context (Coall & Chisholm, 2003), which makes it difficult to isolate causal factors (Chen, Miller, Kobor, & Cole, 2011). Both maternal stress and early adversity often extend into the postnatal child-rearing period (Hackman et al., 2010; Janevic et al., 2010). This issue can be addressed in an animal model by randomly assigning pregnant females to prenatal disturbance conditions in a controlled laboratory setting. Our analyses took advantage of a unique behavioral dataset that had been generated by observing mother-infant behavior of rhesus monkeys across multiple siblings for 2 decades (Coe & Lubach, 2000; Coe & Shirtcliff, 2004; Coe, Lubach, Crispen, Shirtcliff, & Schneider, 2010). Each mother had birthed infants after both undisturbed pregnancies and ones that included periods of moderate or intermittent disturbances (Coe & Lubach, 2005; Coe et al., 2010). The husbandry procedures were standardized; the rearing environment was identical across this 20-year period, and we examined only normal birth weight infants from unassisted natural deliveries.

One aim was to characterize dyadic behavioral interactions and discern the extent to which the mother or infant governed the course toward independence. We hypothesized that both mothers and infants would contribute to dyadic interactions (Bornstein et al., 2003). Second, we determined how mother-infant interactions were affected by a prior history of prenatal disturbance. We predicted that disturbances would impact some dyads more than others. The critical hypothesis was that a mother's intrinsic maternal disposition would influence how

she cared for a prenatally disturbed infant. Analyses controlled for infant sex because monkeys may respond differently to male offspring (Mitchell, 1977, Simpson, 1983), and males may be more susceptible to prenatal disturbance than females (Coe & Crispen, 2000, Geschwind & Galaburda, 1985). We also considered the effect of birth order (Hertwig et al., 2002) after excluding all primiparous births because of known differences in the care shown by inexperienced mothers (Hooley & Simpson, 1981; Seay, 1966; Fleming, Ruble, Kreiger, & Wong, 1997) as well as the change in parenting quality as mothers reach the end of their reproductive years (Hrdy, 1999).

Methods

Subjects

The rhesus monkeys (*Macaca mulatta*) were from an established breeding colony maintained in the same facility for 8-10 generations. Each year, 80-100 new infants are generated from an adult population of approximately 25 males and 150 females. These analyses focused on the behavioral development of 121 infants born to 35 dams over roughly 20 years. Inclusion criteria required that a female be multiparous, deliver healthy offspring naturally, and have birthed a minimum of 3 siblings, which were generated from both undisturbed and experimentally manipulated pregnancies (spaced approximately 1-2 years apart). As described above, primiparous mothers were excluded; final analyses included 2-6 offspring per female. Each infant was reared without concurrent influences from siblings or fathers in order to avoid effects of alloparenting and resource competition (Hrdy, 1999). Twenty adult males sired these infants, with only 4 fathering more than 8 infants. The breeding was controlled, but random with respect to female parity, $p > .09$, and the experimental conditions, $\chi^2(21) = 28.1$, $p = .137$ for MPD and $\chi^2(21) = 20.2$, $p = .09$ for IS. Thus, paternity did not directly contribute to infant behavior observed after birth.

The Harlow Primate Laboratory has cared for these monkeys for more than 5 decades and thus even the dams were born and reared in this facility. Housing conditions are standardized and were identical for all mother-infant pairs. The monkeys lived in one of two housing rooms during the entire study period; the light: dark schedule was 14:10; ambient temperature was set at 21 °C. A fixed number of biscuits were provided in the early morning and late afternoon, which obviated the influence of competing demands on the mother to find food and uneven nutritional status across dyads. In addition, foraging boards, manipulanda, toys, and mirrors were routinely provided as part of an environmental enrichment program, which contributed to the onset of infant exploratory behavior. This degree of control over environmental conditions could not be achieved in humans, nor is it even that common in primate colonies where animals are often bred in less controlled settings. It also enabled us to observe and record the behavior of each mother-infant pair in identical settings over a 20-year time period.

Procedures

Each female was bred with single sire using a timed-mating protocol that permitted precise designation of the father, date of conception, and determination of gestation length. Different sires were used across pregnancies so that the comparison siblings were half-

siblings, but gestated and reared by the same mother. The fathers were randomly assigned to sire infants from control and stressed pregnancies. At specific points during some pregnancies, females were assigned to a disturbance condition and manipulated intermittently. They were then left undisturbed to deliver at term and rear their infants without any further manipulations. Infants were generated from 3 distinct types of pregnancy conditions:

Undisturbed control pregnancies—Other than the initial 4-7 day mating period and routine husbandry procedures for cage cleaning, the gravid female was not disturbed or moved during her pregnancy. She delivered vaginally without human assistance in a familiar 1m³ home cage, which also served as the stable rearing environment for her infant.

Moderate Prenatal Disturbance (MPD)—During this pregnancy condition, a gravid female was moderately disturbed, either on several occasions or in a more sustained manner for up to 2-weeks. The dams had served as experimental controls for several projects, in order to evaluate the influence of the moderate disturbance of handling procedures. They had either experienced small blood sample collections on 4-7 different days, were administered an intramuscular injection of saline or ketamine acutely on 2-4 occasions, or were relocated to a new cage for 2 weeks before being returned to their familiar home cage. Both relocation to novel settings and handling procedures are known to be moderately arousing for laboratory animals that have been acclimated to relatively invariant housing conditions. There were no further experimental manipulations during the last month of pregnancy and they delivered naturally in a manner identical to the undisturbed condition.

Intermittent Stress (IS)—The third pregnancy condition was designed to be more stressful, and involved a controlled disturbance using an acoustical startle protocol. On a daily basis for 6 weeks, or 25% of the 24-week pregnancy, the gravid female was relocated briefly to a darkened room where a computer program broadcast 3 loud noises (1 sec, 110 dB) randomly during a 10 -min period (Coe et al., 2003). This protocol induces a transient activation of the hypothalamic-pituitary-adrenal axis. The stress induction occurred either early (Days 50-92) or late in pregnancy (Days 105-147). For the current analyses, the early and late stress conditions were considered together and designated as Intermittent Stress (IS). Previous research has established that these daily manipulations elevate the gravid female's cortisol levels for several hours, and can affect the development of the brain and immune system in the offspring. Females were not disturbed further during the last month of gestation.

Assignment to conditions

To be included in the current analyses, a female had to deliver healthy, full-term infants both from an undisturbed pregnancy *and* at least one or both disturbance conditions. Across years, the sequence of assignment was purposefully scheduled to alternate between a control and disturbed pregnancy, and the order of pregnancy conditions was counterbalanced across females. Thus, all females birthed sibling monkeys from both types of pregnancies, spaced a minimum of one year apart. The prior infant was always weaned from the mother at 6-8 months of age, several months before the next timed-mating with an adult male. Thus, the

previous infant was not present during the subsequent pregnancy or during behavioral observations of its younger sibling(s).

Behavioral observations

The monkeys' behavior was recorded on a laptop computer when infants were between 2-4 months of age, a dynamic and sensitive period in infant development. After observers acclimated the pair to their presence, a set of defined behaviors were scored during a 5-min period, once per day, 12 times per month. For these analyses, 12 behavioral records were summed to generate one-hour monthly scores for the dyad (duration or frequency/hour). Three behavioral indicators of maternal solicitude were selected: (1) Mother-Infant contact, sustained ventral-ventral contact between mother and infant measured as % of time per session; (2) Maternal Groom, mother manually picks at and or spreads the fur of the infant measured as % of time per session; (3) Maternal Retrieve, infant breaks contact and mother attempts to re-establish contact measured as frequency per hour. Two behaviors reflective of infant autonomy were chosen: (1) Infant Return, infant re-initiates contact with mother after being independent measured as frequency per hour and 2) Infant Exploration, any oral or manual manipulation or exploration of the environment, excluding eating and drinking measured as % of time per session.

Most observations over this 2-decade period were conducted by one observer (HC). Reliability greater than $\kappa=.90$ was achieved for each behavior with 4 research assistants for a minimum of 5 sessions for each assistant. Further quality control was obtained by only including behaviors expressed frequently by most mother-infant pairs, and sufficiently defined and overt that observers consistently scored them similarly. The absence of temporal drift over the 20 years was confirmed as the year of birth for each offspring was uncorrelated with each behavioral score, average $r=.045$, average $p=.57$, $ps>.055$.

Analytic Strategy

A series of Hierarchical Linear Models (HLM) determined the relative contribution of the mother and her offspring to these dyadic behaviors. HLM can model the inherent dependency of multiple siblings within the same family. Level 1 revealed offspring-specific behavior (or unique mother-infant behaviors) and level 2 captured how consistent a mother was across all her offspring for each behavior. The Maternal Groom behavior provides an illustrative example. Each infant's Maternal Groom score was the outcome variable at level 1 (Y_{MG}) to capture how frequently each offspring received grooming from their own mother. To capture a mother's interactions with her offspring from one infant to another, we calculated the intra-class correlation (ICC), the ratio of variance at the mother-level (U_0) with respect to the total variance in that behavior across mothers and offspring (U_0+r). A significant ICC indicates similarity between an infant and its sibling. Put another way, a mother interacted with that infant in a similar manner to how she cared for all of her offspring. The proportion of variance that is infant-specific (r/U_0+r) includes measurement error and unique mother-infant variance; indirectly, it captures the degree of difference of the mother with one infant in behavioral expression from her other infants.

At level 1, we included the infant's prenatal conditions, including Moderate Prenatal Disturbance (MPD=1; other group=0) and Intermittent Stress (IS=2; other group=0) as dummy group variable predictors. Each mother in this sample had multiple offspring, but her offspring had to be from different pregnancy conditions (e.g., one undisturbed pregnancy and at least one moderate-prenatal disturbance and/or intermittent-stress pregnancy). These inclusion criteria permitted us to detect whether a mother interacted differently with offspring generated from her disturbed pregnancies compared to how she interacted with her offspring generated from her undisturbed pregnancies. After simultaneously including both moderate prenatal disturbance group ($\beta_{1\text{MPD}}$) and intermittent stress ($\beta_{2\text{IS}}$), the intercept captured the expected score for an offspring from an undisturbed pregnancy (β_0). Positive coefficient betas (β s) for a pregnancy condition indicate that a mother engaged in more of that behavior with her disturbed than undisturbed infants. Scores are predicted and unstandardized.

For each of the 5 outcome behaviors, main- and interactive effects of pregnancy condition were calculated. To determine whether a pregnancy condition affected each dyad differently, we included the mother's typical behavior averaged across all her offspring as a level 2 predictor of the effect of prenatal disturbance ($\gamma_{11} \cdot \text{TMG}$ for MPD; $\gamma_{21} \cdot \text{TMG}$ for IS). A significant coefficient indicates that the effect of prenatal stress exposure on her dyadic interactions with her infant was dependent on how she typically behaved across all her infants:

Level-1 Model

$$Y_{\text{MG}} = \beta_0 + \beta_{1\text{MPD}} + \beta_{2\text{IS}} + R$$

Level-2 Model

$$\beta_0 = \gamma_{00} + U_0$$

$$\beta_{1\text{MPD}} = \gamma_{10} + \gamma_{11} * (\text{TMG}) + U_1$$

$$\beta_{2\text{IS}} = \gamma_{20} + \gamma_{21} * (\text{TMG}) + U_2$$

Covariates were then added to determine whether effects of prenatal stress exposure were robust. These secondary analyses explored whether mothers interacted differently with her male versus female infants (0=male; 1=female). It then allowed us to compute whether mothers interacted differently with infants as the mother became more experienced with increasing parity and age (0=second offspring and 1 added for each subsequent offspring).

Results

In keeping with expectations, the behavior of the mother and infant underwent significant maturational change across the second and third months following birth. The time the dyad spent in contact declined from an average 70% of the observation to 50% (see Figure 1), $t(120)=11.01$, $p<.0001$. Similarly, maternal grooming of the infant decreased, $t(120)=3.08$, $p<.003$, and mothers were less likely to anxiously retrieve their departing infants by Month 3

as their offspring became more independent, $t(120)=2.47$, $p<.015$. The infant's growing autonomy was further reflected by more time spent in exploring the environment, $t(120)=5.42$, $p<.0001$, and by the fact that its return to the mother, rather than her retrieval behavior, was now accounting for the reestablishment of contact and nursing (Figure 2), $t(120)=6.18$, $p<.0001$.

How much of the dyadic interaction is due to the mother or infant?

To address this question, variation in behavioral interactions was examined across all mothers and infants, and then, whether the variance was mother-specific or infant-specific using the ICC.

Table 1 shows the mother-specific or infant-specific variance for each behavior. The infant contributed to the dyadic interaction, yet the mother demonstrated significant consistency in her behavior across all of her offspring. This stability was more apparent for maternally solicitous behaviors (Mother-Infant Contact, Maternal Grooming, or Maternal Retrieve) than for the infant autonomous behaviors (Infant Return and Infant Exploration). Moreover, the contribution of the mother was more pronounced and consistently significant when the infant was 2 months of age than when it had matured to 3 months of age, with the exception of Infant Return.

Because the ICC was significant for the majority of behaviors, we then examined systematic differences between mothers and between offspring within a matriline. The analyses also tested whether prenatal disturbance, infant gender or birth order affected dyadic behavioral interactions.

Did moderate or intermittent prenatal stress influence interactions between mother and infant?

A series of models addressed this question using the pregnancy condition from which an infant was gestated as a within matriline (level 1) predictor with the Moderate Prenatal Disturbance (MPD) and Intermittent Stress (IS) slopes capturing how the offspring exposed to moderate disturbance or intermittent stress, respectively, diverged from their undisturbed siblings.

There were few initial main effects of MPD (see table 2) or IS (see table 3) on dyadic behavioral interactions at 2 months, and again when offspring were 3 months of age, indicating that the experimental manipulations of pregnancy did exert unidirectional and lingering effects on the mother-infant relationship in the same way. One exception was a main effect of MPD on Infant Return behavior at 2 months of age, $p<.0001$, and 3 months of age, $p<.0001$. Compared to their undisturbed siblings, infants reared after MPD pregnancies returned to their mother more often (see table 2). Conversely, there was a trend for low infant-return at 2 months after IS pregnancies, $p=.064$ (see table 3).

Did prenatal stress influence dyadic interactions differentially depending on a mother's typical behavior?

Given that the ICC indicated each mother evinced an idiosyncratic style of care and the main aim was to compare information on multiple infants from different pregnancy conditions, a series of models were set up to examine Pregnancy Condition as a level 1 predictor (i.e., a predictor of differences between siblings within a matriline). The mother's typical dyadic behavior was examined as a level 2 moderator of any effect of pregnancy disturbances.

This cross-level interaction was statistically significant across behaviors in a consistent manner, all $ps < .0001$, indicating that many mothers treated offspring from MPD or IS pregnancies differently than their undisturbed siblings. However, the direction of this modified care was dependent upon how a mother typically treated all of her infants (see tables 2 and 3). Mothers increased the expression of certain behaviors toward infants generated from MPD pregnancies when they typically exhibited that behavior more than other females. Conversely, following a MPD, those females that showed the lowest level of maternally responsive behavior were likely to decrease those behaviors even further. This pattern was evident when the offspring was 2 months and again at 3 months of age. A significant accentuation of the maternal care style was also evident after IS pregnancies, all $ps < .03$.

Figure 3 illustrates the effects of MPD and IS exposure on dyadic behaviors at the second and third months, focusing first on the maternally solicitous behaviors [Mother-Infant Contact, Maternal Grooming, and Maternal Retrieve]. When offspring were two months of age (grey lines), mothers who were typically low on a behavior engaged in even less of that behavior when rearing a MPD or IS offspring as compared to the undisturbed control offspring (diamond symbol). Conversely, a particular behavior was observed more often when females reared an MPD or IS offspring (square symbol) if the mother was a typically responsive and expressive female. This bidirectional effect based on typical maternal style was especially pronounced for the MPD condition. The interaction between prenatal condition and maternal style was also evident when offspring were 3 months of age (black diamonds and circles, respectively).

Figure 4 illustrates the effect of prenatal disturbance on the two autonomous infant behaviors [Infant Return and Infant Exploration]. As with the maternally solicitous behavior, there was more Infant Return and Infant Exploration at 2 or 3 months of age (gray and black lines, respectively) when infants were reared by a highly interactive mother (squares and circles, respectively) following MPD than undisturbed pregnancies.

Did the mothers interact differently with male and female offspring?

It was possible that the sex of the infant also influenced mother-infant behavior. We analyzed whether mothers interacted differently with her sons than daughters using infant sex as a level 1 predictor of the dyadic behavior score and as a cross-level interaction with typical maternal behavior.

Table 4 illustrates that for the majority of models, there was no effect of sex, nor were there interactions between infant sex and a mother's typical behavior. One exception was a main

effect of infant sex on Maternal Grooming at 3 months of age, $p=.048$, and an interaction between infant sex and mother-typical grooming score, $p=.021$. Mothers groomed males less than her female offspring when they were typically high grooming mothers. In contrast, mothers groomed sons more than their sisters when typically low grooming mothers. Another exception was that by 3 months of age, there was an interaction between infant sex and Infant Return, $p=.025$. Daughters returned to her mother more frequently than sons, but only if the mother typically raised high Infant Return monkeys. Males returned to their mothers more than their sisters if their mothers typically had low Infant Return offspring.

We then determined whether the previously observed bimodal effects of prenatal stress that were dependent upon maternal style persisted after controlling for infant sex. MPD, IS, and infant sex were the level 1 predictors, and typical maternal behavior was a level 2 predictor of pregnancy condition and sex of infant. There were independent and significant effects of infant sex on the same behaviors as described above for Maternal Grooming at 3 months of age (sex effect, $p=.029$ and sex*typical Maternal Grooming, $p<.0001$), and also with the rate of Infant Return at 3 months of age (sex*typical Infant Return effect, $p=.046$). But more importantly, the effect of group and maternal typical behavior persisted across all five dyadic behaviors at both 2 and 3 months of age, $ps<.031$, indicating the prenatal disturbance effects remained significant after accounting for the smaller influence of infant sex.

Did birth order affect maternal behavior typically shown toward infants?

A parallel set of models examined the main effects of birth order and cross-level interactions between birth order*typical maternal behavior. Table 5 illustrates a main effect of birth order only on Maternal Grooming behavior at 2 months of age, $p=.011$, and 3 months of age, $p<.0001$; mothers groomed later-born siblings more than their earlier-born infants. However, there were significant interactions between birth order and typical mother behavior for all five dyadic behaviors, both at 2 and 3 months of age, $ps<.026$. The nature of these interactions was similar for all behaviors. Maternal Groom is representative of this finding. When a mother was typically a low groomer, she engaged in the least grooming behaviors with earlier-born offspring as compared to her subsequent infants. Conversely, a high grooming mother engaged in the most grooming behavior with her earlier-born offspring and lessened this behavior after her subsequent infants.

We determined whether the effects of MPD and IS remained after controlling for birth order. Cross-level interactions between mother-typical behavior and the MPD condition $ps<.0001$, or IS condition, $ps<.001$, were still significant across all dyadic behaviors, with one exception. The interaction between Typical Infant Exploration*IS at 3 months of age was diminished, $p=.171$. Thus, the strength and consistency of the moderating influence Mother Typical Behavior remained evident in analyses that included birth order or sex of infant, thereby taking into account other changes that occurred with the passage of time and experience across the full complement of her offspring.

Discussion

Our analyses of mother-infant behavior spanning nearly 2 decades demonstrate that mother and infant monkeys, like humans, each make unique contributions to the dyadic relationship

(Gunnar et al, 2007), but that some parenting attributes are also stable across siblings. This conclusion concurs with research showing that population variation in mother-infant interactions depends upon several characteristics, including maternal-typical behavior (Weaver, Richardson, Worlein, De Waal, & Laudenslager, 2004), infant temperament (Coe et al., 2010; Mantymaa et al., 2006; Roughton, Schneider, Bromley, & Coe, 1998) and environmental context (Ellis et al., 2012). Studies in rodents have revealed how variation in maternal care can have far-reaching consequences on emotional reactivity and brain development, which may continue to be manifest even in subsequent generations (Champagne & Meaney, 2007). Our analyses of monkeys were notable in being able to quantitatively delineate how much mothers retain their behavioral dispositions across multiple offspring and following adverse pregnancy conditions. Mothers were distinctive in how each treated their infants, which influenced the speed at which the developing infant matured toward autonomy and was confident in departing and exploring the environment. This individual variation in maternal style also had a marked influence on the effects of prenatal disturbance. Our findings indicate that adversity does not impair the postnatal behavioral development of all infants in the same unidirectional way (Parker, Bundlass, Schatzberg, & Lyons, 2006). Rather, each female's typical manner of caring for her offspring strongly influenced how the effects of prenatal disturbance were manifest, appearing to accentuate each female's intrinsic disposition to infant care.

How much of the dyadic interaction is attributable to the mother?

On average, the infant or unique aspects of a particular mother-infant pair accounted for a large proportion of the variance in dyadic behavior. Yet, each mother also demonstrated a high degree of consistency in her caregiving behavior across multiple offspring. This maternal contribution was more apparent when each of her infants was 2 months than when they had matured to 3 months of age. One exception to this age trend was seen for Infant Return behavior, for which the mother's influence was greater at 3 months of age, perhaps because her prior care now influenced the propensity of the more autonomous but still reactive infant to return (Kaye & Fogel, 1980; Hinde & White, 1974). Studies in rodents illustrate how early maternal care can also have delayed effects, and the dramatic effects of maternal licking and grooming appear latent in the very young pup (Meaney & Szyf, 2005). As infants grow to be more independent, and can more actively contribute to the dyadic interactions, behavioral responses then become more consistently evident (Bornstein & Tamis-LeMonda, 1990; de Weerth & van Geert, 2002; Hsu & Fogel, 2003; Lavelli & Fogel, 2002). Our observations did not track the developmental trajectory through weaning at 5-6 months, but instead focused on the most dynamic period when the infant first begins to engage in independent exploration of its environment. This period of development encompasses the stage when leaving and return behaviors are common, including maternal retrievals, with both parties acting as active contributors to the dyadic interactions. Thus, it is not surprising that at 2 and 3 months of age, large differences in maternal style were clearly evident.

Does prenatal stress influence interactions between mother and infant?

Mother-infant interactions were not perturbed by prenatal disturbance in a simple manner that affected all dyads equally. In contrast, our findings emphasize the significance of each

female's own intrinsic disposition toward motherhood and the importance of contingent mother-infant interactions (Beaulieu & Bugental, 2008). Both the moderate disturbance condition and more sustained stressful manipulations during pregnancy accentuated the inherent maternal disposition of each female. This differential effect was filtered through the idiosyncratic maternal disposition of each female and was observed even though all were full-term, healthy, and normal birth weight infants. Unlike many studies of prenatal stress in rodents where the growth of the pups is stunted and litter size reduced by the procedures, our experimental manipulations were carefully tempered so as not to induce prematurity or impair growth rates. Here it is also important to emphasize that the current findings do not address the compensatory caregiving to infants born premature, at low birth weight, or with disabilities (Lupien et al., 2009). Nevertheless, the implications are substantial because they address how the nurturant behavior of a parturient female can be uniquely influenced by prior events during her pregnancy.

Impact of Sex of Infant or Birth Order on Mother-Infant Behaviors

Although our primary focus was on prenatal disturbance, we additionally assessed whether birth order and sex of the infant influenced the dyadic behavioral interactions. Some prior primate studies have reported that there is differential care of male and female infants (Jensen, Bobbitt, & Gordon, 1966, Mitchell, 1977), but these effects typically are not large, nor consistently found across all primate species. In keeping with the view that the effects are modest, maternal care was not strongly affected by the sex of the infant. There was only a small influence on the amount of grooming received by the infant, and a modest influence on Infant Return behavior, which may reflect the tendency of male infants to become more autonomous a younger age. Similarly, there was not a pronounced effect of birth order. Here it should be reiterated that we purposefully excluded the infants of primiparous dams because it is known that their inexperience does result in a large effect on mother-infant interactions. Although parity did not alter the effect of prenatal disturbance, it was of interest that the influence of maternal disposition was more evident in how females cared for earlier-born offspring. This differential effect of birth order was evident in both mothers who engaged in high levels of maternal care as well as in those less interactive with their infants. It may also be that as the adult females had more offspring and became more experienced, older mothers, they were less susceptible to the influence of prenatal disturbance. Over the course of having many infants (a minimum of 2 beyond the first-born and as many as 7), the pervasiveness of the influence of maternal intrinsic disposition appeared to wane. Few studies have considered how parenting style changes over the course of the life span. In humans and many other primates, and reproductive settings, it would be difficult to discern the influence of maternal dispositions because the care would be influenced by the presence of other siblings, periodic instances of infant mortality, and other contextual changes (Schlomer, Del Giudice & Ellis, 2011).

The stability of the standardized housing conditions and controlled nature of experimental manipulations during the pregnancy period helped to reveal the consistent style of care exhibited by these female monkeys. However, notwithstanding the uniqueness of this dataset, there are some notable limitations. Although the infants were sired by 20 different father, thereby minimizing genetic confounding across siblings (i.e., most were half-

siblings), the mother was obviously related to each infant. Genetic influences may have contributed to the appearance of a consistent developmental and maternal care profile for related infants (see Capitanio et al., 2011). It might seem preferable to have cross-fostered infants to an unrelated female as commonly done in rodent studies, but the practice introduces its own problems in a primate study. Adoptions in rhesus macaques are successful only with select females who are especially solicitous caregivers; thus fostering would constrain natural variation in maternal care to only a subset of the most nurturant mothers and functionally exclude one of the most interesting types of mothers (from a policy vantage point) who might actually decrease dyadic infant interactions when rearing a prenatally disturbed infant. This methodological issue parallels the challenge of range restriction in adoption studies with children (Stoolmiller, 1999). Third, the respective influence of the infant and mother to shared interactions can never be totally disentangled. Our experimental design and statistical modeling provided one means to discern the consistency of the maternal contribution across her infants. It should also be reiterated that the prenatal disturbances were purposefully assigned in a balanced manner across females, never occurring during two successive pregnancies. Thus, neither experimental order nor maternal age and experience contributed to our finding that prenatal disturbance accentuated the inherent predisposition to engage in relatively high or low levels of caregiving. Fourth, there is a possibility that siblings were similar due to paternal rather than maternal forces. Paternal influences were minimized given that offspring were half-siblings, sires were randomly assigned to pregnancy type and female, and sires were not housed with the gravid female or child after the timed-mating period. Furthermore, we calculated the ICC based on whether the offspring behaviors were similar if siblings shared the same father (instead of mother). The percentage of variance in mother-infant behaviors which was stable across siblings with the same father was, on average, 4.5% and was not consistently statistically significant. The only exception was infant explore in which 26% and 24% of the variance in IE was stable across siblings with the same father. Finally, it was unexpected that moderate disturbance during the prenatal period would more prominently bring out the inherent maternal caregiving propensities (Coe et al, 2003). In keeping with the growing awareness of nonlinear effects with stress and environmental conditions (Del Giudice et al, 2011), it is possible that moderate arousal was more effective at enhancing maternal disposition, but that 6-weeks of sustained stress had its own additional effects on the infant (Bugental & Happeney, 2004). We have previously demonstrated that this type of prenatal stress can affect neural, immune and behavioral development of infant monkeys (Coe et al, 2010; Coe & Lubach, 2003; Coe et al 2003). Thus, the observed changes in maternal responsiveness probably interacted with some differences in the emotional reactivity of the infants from the more potent IS conditions.

In conclusion, our study highlights the importance of a female's intrinsic disposition toward motherhood. These attributes have the potential to exacerbate or mitigate the vulnerabilities of a healthy or compromised infant that were programmed prenatally. Certainly, how caregivers treat the young infant is important in determining whether the effects of prenatal disturbance persist and have long-term effects physical and psychological wellbeing. As Darwin advocated over 150 years ago, maternal rearing strategies are an important aspect of

natural selection among mammals, and help to account for differential infant survival, especially under adverse circumstances.

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1. The 3 graphs illustrate the mean levels (+S.D.) of the mother-initiated components of the observed dyadic behavior when the infant monkeys were two and three months of age.

2.

The 2 graphs portray the mean levels (+SD) of infant-initiated behaviors, infant return to mother and environmental exploration, which contributed to variance in the dyadic interactions when the infant monkeys were two and three months of age.

3. Effects of prenatal disturbance [moderate prenatal disturbance (MPD), and intermittent stress exposure (IS)], as compared to control pregnancies on dyadic behavior when infants were two and three months of age. The graphs focus on the mother-initiated behaviors including Mother-Infant Contact (MI), Maternal Groom (MG) and Maternal Retrieve (MR). High and Low typical maternal behavior are represented as the predicted score in the HLM analysis for a mother who is one standard deviation above and below the mean, respectively.

4.

Effects of prenatal disturbance on two infant-initiated behaviors including Infant Returns to the mother (IR), which results in a dyadic interaction, and Infant Explores of the environment (IE). High and Low IR and IE MOM lines represent the predicted score in the HLM analysis for an infant who is reared by a mother who typically has infants who are one standard deviation above and below the mean, respectively, on that dyadic behavior.

Table 1

Mother-infant dyadic interactions observed when infants were 2 and 3 months of age. Analyses show how much variance in the behavior was attributable to either the mother or infant.

<i>Behaviors</i>	2 Months of Age		3 Months of Age	
	Mother %	Infant %	Mother %	Infant %
<i>Mother-Infant Contact (MI)</i>	32.28 **	67.72	7.97 *	92.03
<i>Maternal Grooming (MG)</i>	36.38 **	63.62	20.82 **	79.18
<i>Maternal Retrieve (MR)</i>	20.26 **	79.74	6.15	93.85
<i>Infant Return (IR)</i>	9.80 *	90.20	17.89 **	82.11
<i>Infant Exploration (IE)</i>	5.62	94.38	0.08	99.91

* p 0.05;

** p<0.0001

NOTE: Significance tests are applied to the mother-specific variance only. This is the Intra-class correlation or degree of consistency in behavioral observations across all her offspring.

Table 2

Main and interactive effects on dyadic behaviors between mother and infant with maternal typical behavior as a within family predictor in the infant's second and third month.

Behaviors	MPD		MPD * Maternal Typical Behavior	
	2 Months β	3 Months β	2 Months β	3 Months β
<i>MI</i>	4.71	7.18	0.82 **	0.53 **
<i>MG</i>	4.22	5.21	0.90 **	1.18 **
<i>MR</i>	-0.09	0.06	0.98 **	0.94 **
<i>IR</i>	10.56 **	18.58 **	1.02 **	1.04 **
<i>IE</i>	-1.56	-1.99	0.85 **	0.93 **

* p .05;

** p<.0001

NOTE: higher β s indicate that offspring from MPD pregnancies exhibit the behavior more than that mother's offspring from undisturbed pregnancies. For infant return (IR) and infant explore (IE), the MPD*Maternal Typical Behavior interactions indicate the degree to which the MPD infant engages in these behaviors against the backdrop of how often their siblings engage in these behaviors.

Table 3

Main and interactive effects on dyadic behaviors between mother and infant with average maternal behavior as a within family predictor when infants are two and three months of age.

Behaviors	IS		IS*Maternal Typical Behavior	
	2 Months β	3 Months β	2 Months β	3 Months β
<i>MI</i>	0.18	0.99	0.37 **	0.30 **
<i>MG</i>	-5.69	1.62	0.25 *	0.42 **
<i>MR</i>	-0.03	0.08	0.48 **	0.56 **
<i>IR</i>	-1.20 ⁺	-1.47	0.15 **	0.13 **
<i>IE</i>	0.98	-0.08	0.12 **	0.26 *

⁺ p<.10;

* p .05;

** p<.0001

NOTE: Higher β s indicate that offspring from IS pregnancies exhibit the behavior more than do infants from that mother's undisturbed pregnancies. For infant return (IR) and infant explore (IE), the MPD*Maternal Typical Behavior interactions indicate the degree to which the IS infant engages in these behaviors in relation to their siblings.

Table 4

Influence of sex of infant on the main and interactive effects on dyadic behaviors between mother and infant when infants were 2 and 3 months of age.

Behaviors	Sex		Sex * Maternal Typical Behavior	
	2 Months β	3 Months β	2 Months β	3 Months β
<i>MI</i>	-3.337	-7.076	-0.236	-0.032
<i>MG</i>	3.623	* 7.956	0.102	* 0.375
<i>MR</i>	0.141	0.040	-0.170	-0.438
<i>IR</i>	1.755	0.728	0.220	* 0.203
<i>IE</i>	2.825	3.211	-0.577	0.305

*
p .05;

**
p<.0001

NOTE: higher β s indicate that these behaviors were shown more when the infant was female than with male offspring.

Table 5

Influence of Birth Order on the main and interactive effects on dyadic behaviors between mother and infant when infants were 2 and 3 months of age.

Behaviors	Birth Order		Birth Order * Maternal Typical Behavior	
	2 Months β	3 Months β	2 Months β	3 Months β
<i>MI</i>	0.222	2.895	– 0.404 **	– 0.343 **
<i>MG</i>	5.705 *	8.026 **	– 0.735 **	– 0.601 **
<i>MR</i>	–0.0003	–0.012	– 0.447 **	– 0.298 **
<i>IR</i>	0.717	–0.265	– 0.086 *	– 0.099 *
<i>IE</i>	–0.186	–0.352	– 0.704 **	– 0.546 **

*
p .05;

**
p<.0001

NOTE: Higher β s indicate that these behaviors were observed more with later born than earlier-born offspring.