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Hormones and behavior in rhesus macaque abusive and nonabusive mothers
2. Mother–infant interactions

Dario Maestripieri[a,b,*], Nancy L. Megna[b]

[a]*Committee on Human Development, University of Chicago, Chicago, IL, USA*
[b]*Yerkes Regional Primate Research Center, Emory University, Atlanta, GA, USA*

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Abstract

This study investigated the differences in parenting style and hormonal variables in abusive and nonabusive rhesus macaque mothers during the first 2 months of lactation. All subjects lived in large social groups in outdoor corrals. Abusive mothers were more protective and more rejecting of their infants than nonabusive mothers, particularly in the first month. Abusive and nonabusive mothers did not differ in levels of circulating estradiol (E2) and progesterone (P) during the periparturitional period except that the decrease in P after parturition was less marked in abusive than in nonabusive mothers. Individual differences in periparturitional E2 or P were not correlated with differences in parenting style. Mothers with higher frequencies of abuse, however, had significantly higher values of the E2-to-P ratio in the last week of pregnancy and significantly lower values of P in the first week of lactation than mothers with lower frequencies of abuse. Although pregnancy or lactation hormones are unlikely to be one of the main determinants of abusive behavior, endocrine variables may interact with personality characteristics or environmental factors in causing this phenomenon.

Keywords: Infant abuse; Maternal behavior; Individual differences; Hormones

1. Introduction

Recent studies of large captive populations of rhesus macaques (*Macaca mulatta*) and other Cercopithecine monkeys have shown that 5–10% of all infants born in a given year are at risk of being physically abused by their mothers [9,11]. Naturally occurring maternal abuse of offspring (i.e. abuse not induced by laboratory manipulations) has also been reported in other captive and wild populations of primates [5,18,21]. Although the exact causes of infant abuse are not well understood, abusive behavior appears to be a stable maternal characteristic. In fact, abusive mothers tend to abuse all of their infants, and individual differences in the frequency and physical patterns of abuse are remarkably consistent over the years [9,14].

The finding that infant abuse runs in families [9,15] suggests that abusive behavior patterns are transmitted across generations through learning mechanisms or in conjunction with biological characteristics, or both. The steroid hormones associated with pregnancy, parturition, and lactation are one of the biological variables that may be potentially associated with maternal abusive behavior. A recent study of pigtail macaques (*Macaca nemestrina*) reported that adult females became more interested in other females' infants in the last few weeks of pregnancy, in conjunction with an increase in plasma estradiol (E2) and in the E2-to-progesterone (P) ratio (E2/P; [16]). In rhesus macaques, administration of exogenous E2 to ovariectomized females significantly increased their rate of interaction with other females' infants [16]. Moreover, in a species of New World monkeys, the red-bellied tamarin (*Saguinus labiatus*), Pryce et al. [17] reported that, among females without previous caregiving experience, mothers whose infants did not survive had lower urinary concentrations of E2 in the last week of pregnancy than mothers whose infants survived. These findings raise

* Corresponding author. Committee on Human Development, University of Chicago, 5730 S. Woodlawn Avenue, Chicago, IL 60637, USA.
E-mail address: dario@ccp.uchicago.edu (D. Maestripieri).

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the possibility that abusive mothers may differ from nonabusive ones in some aspects of neuroendocrine function during the periparturitional period, and that the abusive mothers' hormonal profiles may affect their motivation to interact with infants or the quality of their maternal behavior.

More generally, it is possible that differences in hormone levels may account for individual differences in maternal behavior across both abusive and nonabusive mothers. Three decades of research on mother–infant interactions in rhesus macaques and other Old World monkeys have shown that there is a great deal of intra-population and intra-group variability in parenting styles along the two dimensions of maternal protectiveness and rejection [3]. A previous study comparing the parenting styles of rhesus macaque abusive and nonabusive mothers reported that the former are both more protective and more rejecting of their infants than the latter [6]. Unfortunately, studies investigating the role of hormones or other physiological variables in determining individual differences in parenting styles in Old World monkeys are virtually nonexistent. Thus, the extent to which biological variables interact with social and experiential factors in regulating primate maternal behavior remains unclear.

The aims of the present study were (a) to further characterize the parenting styles of rhesus macaque abusive mothers relative to nonabusive mothers, (b) to assess the extent to which individual differences in parenting styles among both abusive and nonabusive mothers are predicted by differences in periparturitional changes in hormone levels, notably in E2, P, and the E2-to-P ratio, and (c) to investigate variability in hormone levels among abusive mothers in relation to their propensity to adopt an alien infant in a cross-fostering procedure and the severity of their abusive behavior.

2. Methods

2.1. Subjects and procedure

Information on subjects and procedure, including hormonal assays, is provided elsewhere [12].

2.2. Behavioral observations

Behavioral data collection focused on mother–infant interactions, including infant abuse. The following behavior patterns were included in the infant abuse category: (1) dragging: the mother drags her infant by its tail or leg while walking or running; (2) crushing: the mother pushes her infant on the ground with both hands; (3) throwing: the mother throws her infant a short distance with one hand while standing or walking; (4) hitting: the mother violently slaps her infant with one hand or arm; (5) biting: common definition; (6) stepping or sitting on: the mother steps on her infant with one foot or both feet, or sits on her infant; (7) dangling/dropping: the mother climbs a tree or fence and holds her infant by its tail or leg or drops her infant on the ground; (8) rough grooming: the mother pulls her infant's hair or otherwise roughly grooms it causing distress calls. Infant dragging, crushing, throwing, or sitting/stepping on are clearly distinguishable from other behaviors in the maternal and aggressive repertoire, such as those observed during mother–infant weaning conflicts. Therefore, the occurrence of these behavior patterns was used as a criterion to identify abusive mothers. Because hitting and biting sometimes occur during mother–infant weaning conflicts, they were not used for the initial identification of abusive mothers. Abuse events did not last more than a few seconds and therefore were recorded only in terms of their frequency. Infant abuse was recorded as two separate events if there was a transition in the pattern of behavior (e.g. from dragging to throwing) or if there was a pause of at least 10 s during the behavior. Analyses reported elsewhere showed that the five abusive mothers who adopted unrelated infants, abused them with frequencies very similar to those exhibited with their biological offspring in the previous year [13].

In addition to infant abuse, the following mother–infant interactions were also analyzed: Contact = the frequency of contact made and broken by both mothers and infants. Contact was defined as any bodily contact between mother and infant except brief touching or hitting. Grooming = the frequency with which mothers groomed their infants. Grooming was defined as picking or brushing the fur of the infant. A grooming bout was considered to have ended after a 10-s pause in the behavior. Restraining = the frequency with which mothers prevented their infants from breaking contact by holding them by their tail or leg. Rejection = the frequency with which mothers prevented their infants from making contact or gaining access to the nipple by pushing the infant away or blocking the chest with an arm. Contact and grooming were also recorded in terms of their duration, but since frequency and duration data were highly correlated, only frequency measures were reported to avoid redundancy. Based on the findings of previous studies, we predicted that abusive mothers would be more protective and more rejecting of their infants than nonabusive mothers [6,10]. In other words, abusive mothers were expected to score higher than controls on measures of making and breaking contact, grooming, restrain and rejection.

3. Results

3.1. Parenting styles of abusive and nonabusive mothers

Fig. 1 shows the time course of maternal abusive behavior in relation to infant age. Most abusive mothers showed a gradual decline in their frequency of abuse over the 8 weeks of lactation, with the exception of one mother whose frequency of abuse was high throughout the study

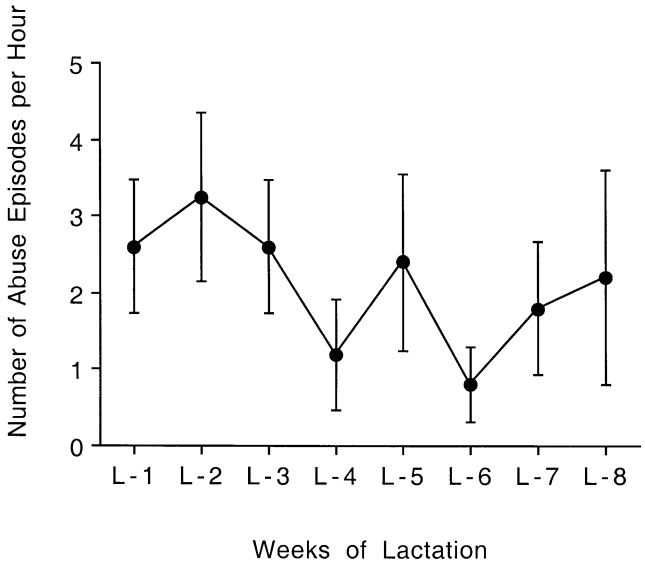

Fig. 1. Mean (±SEM) number of infant abuse episodes per individual per week during the first 8 weeks of lactation ($N=5$).

period and, in particular, in weeks 7 and 8. Overall, there was no significant correlation between infant abuse and infant age.

To investigate differences in parenting styles between abusive and nonabusive mothers, the lactation period was subdivided in two 4-week blocks (referred to as first and second month) and maternal behaviors were compared with repeated-measures ANOVA in each month. Abusive mothers made a higher number of contacts with their infants than nonabusive mothers in the first month [$F(1, 13)=3.82$, $p<0.05$; one-tailed probability; Fig. 2a] but not in the second month. In the first month, the frequency of contacts made by mothers increased with infant age [$F(3, 39)=6.18$, $p<0.01$], although the increase for the abusive mothers was not as gradual as for the controls [$F(3, 39)=2.95$, $p<0.05$; Fig. 2a]. There was no effect of infant age on contacts made by mother in the second month. Infants made contact with their mothers more often as they grew older, particularly in the first month [$F(3, 39)=10.14$, $p<0.001$; Fig. 2b], but there were no significant differences between abused and nonabused infants.

Abusive mothers broke contact with their infants significantly more often than nonabusive mothers in the first month [$F(1, 13)=39.85$, $p<0.01$; one-tailed probability; Fig. 3a], as well as in the second month [$F(1, 12)=3.95$, $p<0.05$; one-tailed probability]. In the first month, contacts broken by mothers increased significantly in relation to infant age [$F(3, 39)=6.46$, $p<0.01$], but such increase was more marked for abusive than nonabusive mothers [$F(3, 39)=3.11$, $p<0.05$]. Infants broke contact with their mothers more often as they grew older, particularly in the first month [$F(3, 39)=9.03$, $p<0.001$; Fig. 3b], but there were no significant differences between abused and nonabused infants.

There were no significant differences in the frequency with which abusive and control mothers groomed their infants in the first or second month (Fig. 4). Grooming, however, varied with infant age to a different extent in abusive and nonabusive mothers [first month: $F(3, 39)=4.54$, $p<0.01$; second month: $F(3, 36)=5.20$, $p<0.01$]. Maternal restraining showed a similar pattern of variation in abusive and nonabusive mothers (Fig. 5a). Abusive mothers, however, restrained their infants more often than controls did in the first month [$F(1, 13)=5.38$, $p<0.05$; one-tailed probability] but not in the second month. Abusive mothers also rejected their infants more than controls did in

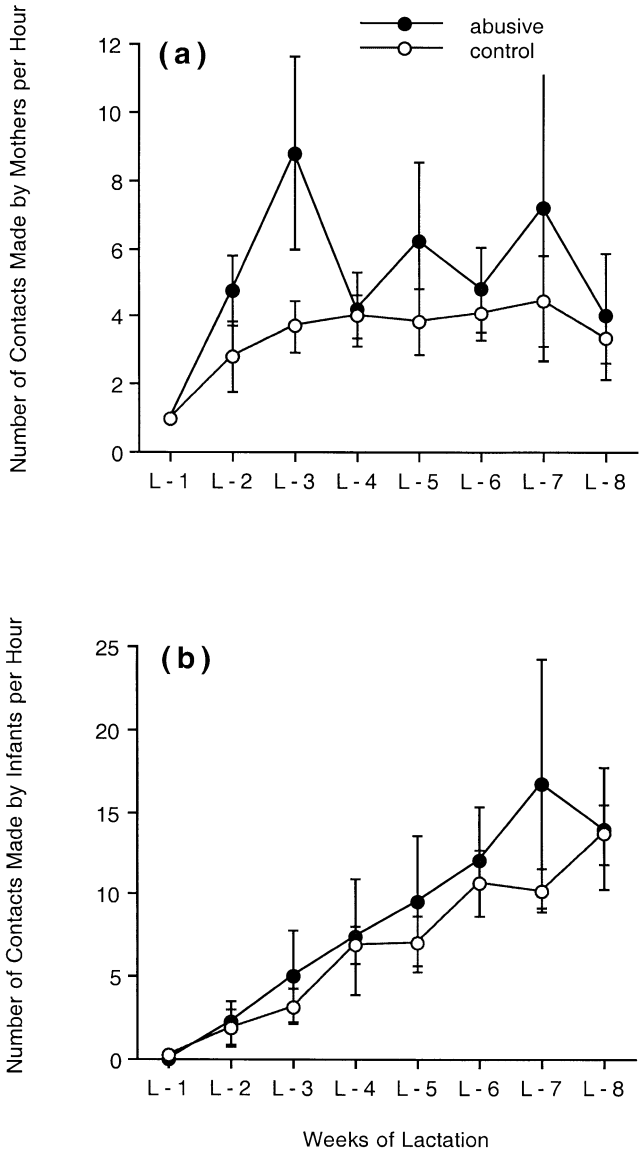

Fig. 2. (a) Mean (±SEM) number of contacts made by mothers per hour per individual during the first 8 weeks of lactation in abusive and control mothers. (b) Mean (±SEM) number of contacts made by infants per hour per individual during the first 8 weeks of lactation in abusive and control mother–infant dyads. Abusive mothers; $N=5$, controls; weeks 1–4, $N=10$; weeks 5–8, $N=9$.

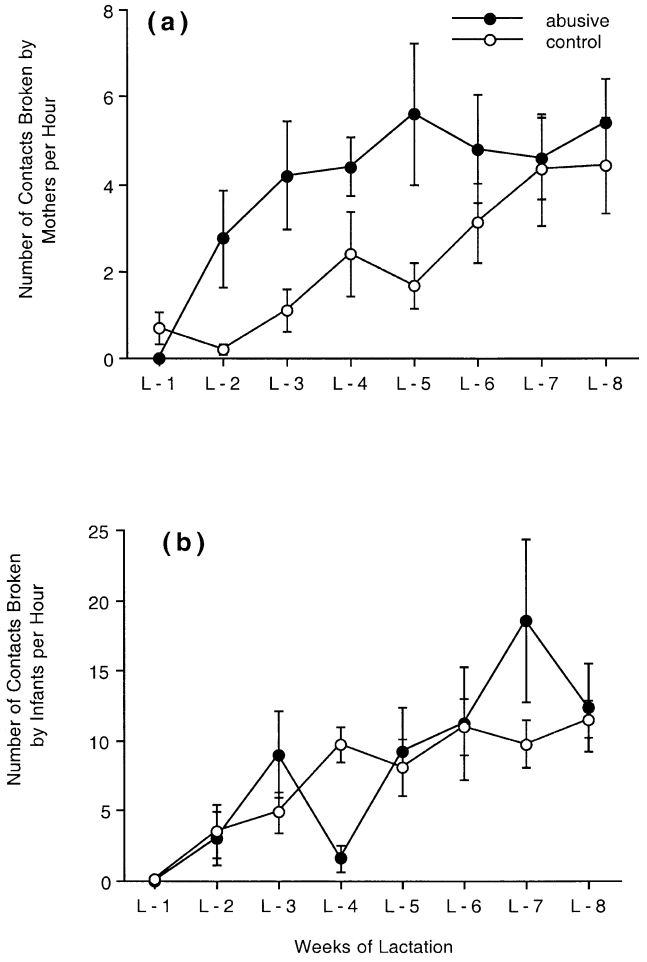

Fig. 3. (a) Mean (±SEM) number of contacts broken by mothers per hour per individual during the first 8 weeks of lactation in abusive and control mothers. (b) Mean (±SEM) number of contacts broken by infants per hour per individual during the first 8 weeks of lactation in abusive and control mother–infant dyads. Abusive mothers; $N=5$, controls; weeks 1–4, $N=10$; weeks 5–8, $N=9$.

the first month [$F(1, 13)=3.65$, $p<0.05$; one-tailed probability] but not in the second month (Fig. 5b).

To summarize, abusive mothers were generally more protective of their infants (e.g. they made contact with them and restrained them more often) as well as more rejecting (e.g. they broke contact with them and rejected their attempts at making contact more often) than nonabusive mothers, and differences in parenting styles were generally more marked in the first than in second month of lactation.

3.2. Hormonal correlates of differences in parenting styles

The following hormonal measures were used as potential predictors of differences in selected maternal behaviors: the levels of E2, P, and the E2/P during the last week of pregnancy and the first week of lactation; the magnitude of the reduction in E2, P, and E2/P after parturition (difference in values between the last week of pregnancy and the first week of lactation); and the mean values of E2, P, and E2/P across the first 4 weeks of lactation (see Table 1). Abusive and nonabusive mothers differed significantly in only one of these measures: the reduction in P levels after parturition was more marked for controls than for abusive mothers (Student's t test for unpaired samples, $t=2.30$, $df=13$, $p<0.05$; Table 1). This significant difference, however, could have arisen by chance because of the number of tests performed. Given the similarities in the other hormonal measures and the small number of abusive mothers, the data from abusive and nonabusive mothers were lumped in subsequent analyses to increase the sample size.

Such analyses did not reveal any significant correlation between hormonal variables and behavioral variables such as the frequency of contacts made and broken by mothers and the frequency of maternal grooming, restraining or rejection.

3.3. Hormones, infant adoption, and infant abuse

The five abusive mothers who successfully adopted an alien infant in the first week after parturition did not differ significantly from the five abusive mothers who rejected the infant in the hormonal variables considered in this study (the levels of E2, P, and the E2/P during the last week of pregnancy and the first week of lactation; the magnitude of the reduction in E2, P, and E2/P after parturition, and the mean values of E2, P, and E2/P across the first 4 weeks of lactation).

Since the number of abusive mothers with infants was too small to investigate variability in hormonal variables in relation to severity of abuse, the frequencies of infant abuse

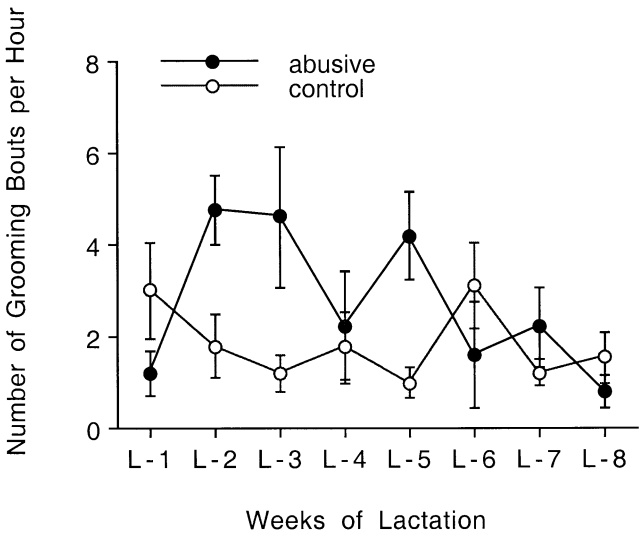

Fig. 4. Mean (±SEM) number of maternal grooming episodes per hour per individual during the first 8 weeks of lactation in abusive and control mothers. Abusive mothers; $N=5$, controls; weeks 1–4, $N=10$; weeks 5–8, $N=9$.

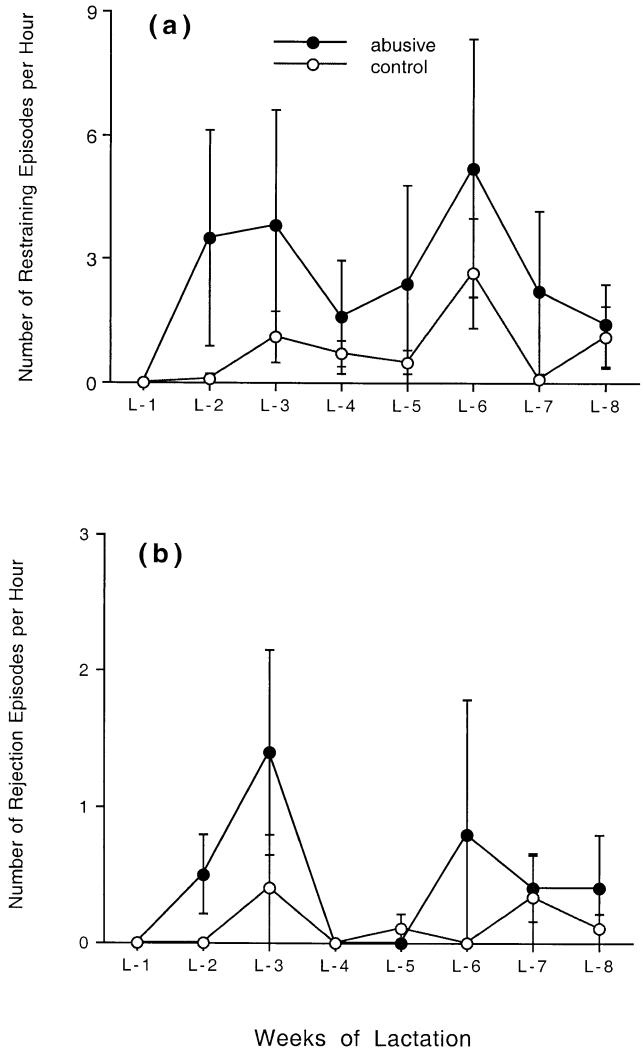

Fig. 5. (a) Mean (±SEM) number of restraining episodes per hour per individual during the first 8 weeks of lactation in abusive and control mothers. (b) Mean (±SEM) number of rejection episodes per hour per individual during the first 8 weeks of lactation in abusive and control mothers. Abusive mothers; $N=5$, controls; weeks 1–4, $N=10$; weeks 5–8, $N=9$.

recorded for all 10 abusive mothers the previous year were used for this analyses, along with hormonal data obtained in this study. In this population, individual frequencies of abuse are highly correlated across successive infants [14] and those displayed by the five abusive mothers who adopted an alien infant were very similar to those of the previous year [13]. When the sample of abusive mothers was split around the median value of abuse frequency in two subgroups (severe abuse, S: $n=5$; mild abuse, M: $n=5$), the S mothers had significantly higher values of the E2/P in the last week of pregnancy ($t=3.26$, $df=8$, $p=0.01$) and significantly lower values of P in the first week of lactation ($t=-3.38$, $df=8$, $p=0.01$) than the M mothers. The S and M mothers, however, did not differ significantly from controls in these endocrine variables.

4. Discussion

The investigation of behavioral differences between abusive and nonabusive mothers during the first 8 weeks of lactation revealed that the former were both more protective and more rejecting of their infants than the latter. Abusive mothers made contact with their infants and restrained them more often than nonabusive mothers did. Abusive mothers also broke contact with their infants and rejected their attempts at making contact more often than nonabusive mothers did. These differences were generally more apparent in the first than in the second month of lactation.

It is very unlikely that the adoption of unrelated infants by abusive mothers may have resulted in differences in maternal behavior between subjects and controls for several reasons: First, all mothers were handled with similar procedures; second, adopted infants were treated by their mothers as if they were their own biological offspring [13]; third, previous studies have shown that mothers with adopted

Table 1
Levels of E2, P, and values of the E2 to P ratio (E2/P) during the last week of pregnancy (P24), the first week of lactation (L1), and across lactation (L) in abusive (abuse) and nonabusive (control) mothers. The difference in hormonal levels between the last week of pregnancy and the first week of lactation (P24 – L1) is also reported. Hormone levels are reported in pg/ml.

	Abuse (mean ± SEM)	Control (mean ± SEM)
E2 (P24)	831.31 ± 75.35	881.19 ± 56.13
P (P24)	478.00 ± 69.83	493.20 ± 76.71
E2/P (P24)	1.94 ± 0.19	2.08 ± 0.28
E2 (L1)	143.44 ± 44.81	115.97 ± 50.13
P (L1)	232.43 ± 49.76	182.10 ± 54.81
E2/P (L1)	0.64 ± 0.14	0.62 ± 0.10
E2 (L)	72.58 ± 16.57	61.16 ± 14.55
P (L)	149.20 ± 37.42	114.40 ± 27.19
E2/P (L)	0.64 ± 0.15	0.59 ± 0.08
E2 (P24 – L1)	616.66 ± 53.39	765.23 ± 77.56
P (P24 – L1)	181.00 ± 34.78	310.80 ± 40.15
E2/P (P24 – L1)	1.31 ± 0.23	1.47 ± 0.26

Number of subjects: P24: abusive = 10, control = 10; L1: abusive = 5, control = 10; L: abusive = 5, control = 9.

infants are behaviorally undistinguishable from mothers with biological offspring [2,19,20]; finally, the behavioral differences between abusive and nonabusive mothers reported here are entirely consistent with those reported in a previous study [6]. Therefore, it is reasonable to argue that the differences reported here were not confounded by particular experimental procedures.

The changes in levels of E2, P, and in the E2/P during late pregnancy and early lactation were described in detail elsewhere [12]. The analyses conducted in this study focused on the periparturitional changes in hormone levels, as these changes may be the most relevant to maternal behavior, including infant abuse. Abusive mothers were generally similar to nonabusive mothers in their hormone levels before and after parturition, with the exception that the reduction in P after parturition was more marked for the controls than for the subjects. When data from the abusive and nonabusive mothers were lumped together, no significant correlation emerged between periparturitional hormonal changes and individual differences in maternal behavior. Thus, the extent to which rhesus mothers are protective or rejecting of their infants seems to be unrelated to quantitative differences in the endocrine events of the periparturitional period, at least those involving E2 or P. In fact, it cannot be ruled out that other hormones or neurotransmitters such as prolactin, cortisol, oxytocin, or beta-endorphin may be better predictors of variability in maternal behavior than E2 and P [1].

The five abusive mothers who adopted alien infants did not differ from the five mothers who rejected them in any of the hormonal measures considered in this study. This suggests that (a) the propensity of adopt an alien infant in a cross-fostering procedure is a good indicator of maternal motivation, but differences in maternal motivation are not predicted by hormonal variables, at least not those considered in this study, or (b) individual differences in the propensity to adopt infants do not reflect differences in maternal motivation but in sensitivity to the stressful components of the experimental procedure (e.g. capture, separation from offspring, exposure to an alien infant). In this case, no relation between pregnancy or lactation hormones and propensity to adopt infants would necessarily be expected.

The analysis of variability in hormone levels in relation to the severity of abuse was constrained by the small number of abusive mothers and, therefore, by the fact that in order to increase the sample size, data on infant abuse collected the previous year were used. When the sample of 10 abusive mothers was split in relation to frequency of infant abuse, mothers with higher frequencies of abuse had significantly higher values of the E2/P in the last week of pregnancy and significantly lower values of P in the first week of lactation than mothers with lower frequencies of abuse. These findings suggest that there may be a relation between abusive behavior and periparturitional hormones but that such relation may be apparent only in the most abusive mothers. Interestingly, Fleming et al. [4] reported a correlation between the E2/P in late pregnancy and both postpartum feelings of attachment to the infant and maternal mood in human mothers. Thus, the relation between periparturitional hormones and abusive behavior in monkeys could be mediated by the mother's caregiving motivation, her emotional status, or both. Clearly, before any firm conclusions can be drawn, these preliminary findings must be replicated and extended by future studies in which hormonal variables are experimentally manipulated.

Establishing that individual differences in primate maternal behavior are, at least in part, accounted for by hormonal variables is a challenging task that will require a great deal of future research effort. This is because individual differences in primate parenting are affected to a great extent by previous experience and the surrounding environment [7]. Cognitive and social factors can interact with biological variables in a complex fashion or, in some cases, override their effects. Similar to child abuse, infant abuse in nonhuman primates is probably a complex and heterogeneous phenomenon in which biological variables may interact with experiential and environmental factors [8,11]. For example, the changes in social behavior accompanying motherhood in abusive and nonabusive individuals (e.g. the finding that abusive mothers become less affiliative and more aggressive toward other individuals to a greater extent than nonabusive mothers [12]) may suggest that motherhood is more stressful in the former than in the latter individuals. This, in turn, may be due to differences in biologically based personality characteristics of abusive and nonabusive mothers or in the amount of social support provided to them by their networks of kin and allies. It is also possible that infant abuse is the outcome of multiple pathways so that biological variables play a larger role in the causation of abusive behavior in some individuals than in others. For example, the correlation between endocrine variables and severity of abuse suggests that, in the most abusive individuals, vulnerability to stress may also interact with deficits in the maternal motivation system. Therefore, although hormones are unlikely to be one of the main determinants of abusive behavior, they should nevertheless be taken in consideration by future research investigating the causes of this phenomenon.

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