ELSEVIER

Physiology & Behavior 71 (2000) 35–42

PHYSIOLOGY & BEHAVIOR

Hormones and behavior in rhesus macaque abusive and nonabusive mothers 1. Social interactions during late pregnancy and early lactation

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*

Received 17 March 2000; received in revised form 11 May 2000; accepted 15 May 2000

Abstract

This study investigated changes in hormone levels and social behavior during late pregnancy and early lactation in rhesus macaque abusive and nonabusive mothers. All subjects lived in large social groups in outdoor corrals. Estradiol and progesterone levels increased to a peak the week before parturition, dropped after parturition, and remained low thereafter. The hormonal profiles of abusive and nonabusive mothers were generally similar. There were few changes in social interactions involving contact, grooming, or aggression across pregnancy or lactation, and minor differences between abusive and nonabusive mothers. The transition to motherhood was accompanied by a reduction in active grooming and an increase in aggression, and such changes were more marked for abusive than nonabusive mothers. Some individual differences in social behavior were correlated with hormone levels during pregnancy, but not lactation. These findings suggest that although the endocrine changes underlying the periparturitional period may affect female social behavior, some of the social changes associated with motherhood are likely to reflect the presence of infants.

Keywords: Pregnancy; Lactation; Social behavior; Infant abuse; Hormones

1. Introduction

In rhesus macaques (*Macaca mulatta*) and other Old World monkeys, the hormonal changes underlying the menstrual cycle are accompanied by dramatic changes, not only in sexual behavior, but also in affiliation and aggression. For example, the late follicular phase of the cycle is characterized by an increase in female–male affiliation and female–female aggression, whereas the luteal phase is accompanied by reduced interactions with males and increased affiliation with females [18]. Some of these changes in social behavior are likely to be directly affected by hormonal fluctuations, whereas others are likely to be the byproduct of other behavioral changes. For example, there is some evidence that the periovulatory increase in female grooming is directly linked to ovarian hormones [15], whereas the luteal phase increase in female–female affiliation may be the result of hormonal changes or be interpreted as a compensation of previous disruption in social relationships [18].

Although hormonal and behavioral changes across the primate menstrual cycle have been thoroughly investigated, considerably less is known about other stages of the reproductive cycle such as pregnancy, parturition, and lactation. First, only a few studies have investigated the periparturitional changes in hormone levels in Old World monkeys. In rhesus macaques, preliminary studies indicated that both estradiol and progesterone peak during late pregnancy and drop immediately after parturition [2,3,19]. Such studies, however, did not describe in detail the pattern of change of these two hormones over late pregnancy and early lactation and/or used a relatively small number of animals. Second, studies in which periparturitional changes in social behavior were investigated in relation to hormonal changes are almost nonexistent. The only study in which both hormones and social behavior were longitudinally investigated across pregnancy was conducted with pigtail macaques, *Macaca nemestrina* [9]. Third, although there are

* 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).

0031-9384/00/$ – see front matter
PII: S0031-9384(00)00337-1

considerable quantitative differences among individuals in both hormone levels and behavior across pregnancy and lactation [9], no study to date has attempted to test whether individual differences in social behavior are predicted by differences in hormones.

A recent study of rhesus macaque mothers who physically abused their infants revealed several marked differences between these individuals and nonabusive mothers in their social interactions with other group members during the first 12 weeks of lactation [8]. Abusive mothers interacted with other females' infants more often and were more aggressive toward other adults than nonabusive mothers. Furthermore, abusive mothers received a lower number of contacts and approaches by other individuals than nonabusive mothers did. These differences were not accounted for by obvious differences in social and demographic characteristics such as dominance rank or age. The question thus arises as to whether some of the differences in the social behavior of abusive and nonabusive mothers may be associated with differences in hormones or other biological variables. For example, there is evidence that higher frequencies of interaction with infants during late pregnancy are associated with higher levels of estradiol in pigtail macaques and that the administration of estradiol to ovariectomized rhesus females significantly increases their interest in infants [13].

The aims of this study were: (a) to investigate changes in social interactions and hormones (estradiol, progesterone, and the estradiol-to-progesterone ratio) during late pregnancy and early lactation in a relatively large number of rhesus macaque females, thus expanding our knowledge of basic behavioral and endocrine processes in this species; (b) to investigate similarities and differences between abusive and nonabusive mothers in both social behavior and hormone changes during late pregnancy and early lactation; and (c) to test whether individual differences in hormonal variables were correlated with differences in social behavior during late pregnancy and early lactation across both abusive and nonabusive mothers.

2. Methods

2.1. Subjects and housing

Subjects of this study were 20 adult female rhesus macaques living in four social groups at the Field Station of the Yerkes Regional Primate Research Center in Lawrenceville, GA. The groups were housed in 38×38 m outdoor compounds with attached indoor areas and consisted of two to five adult males and 30–35 adult females with their immature offspring. The groups were fed monkey chow twice daily (at 0900 and 1500 h) and fruit once daily (1500 h). Water was available ad libitum.

The size and composition of rhesus groups at the Yerkes Field Station approximate those found in the wild [5]. Females spend their entire life in their natal groups while males are removed from their groups and introduced into a different group at puberty to simulate the natural process of male migration and reduce the chances of inbreeding. There is a distinct mating season from September–October to February–March, and a birth season beginning in March and ending in June–July. The dominance ranks of all adult females were assessed with data on aggression, submission, and displacements collected prior to onset of the study. The dominance hierarchy in each group was linear and did not change during the course of the study. Each adult female was classified as high-, middle-, or low-ranking depending on whether her dominance rank fell into the upper, middle, or bottom third of her group's hierarchy.

The adult females ranged in age from 6 to 15 years and were all multiparous, having delivered at least one offspring prior to this study. Ten females had a well-known history of maternal abuse of offspring. They had abused all of their previous offspring (at least, all offspring for which information was available) and their abusive behavior in the past few years had been documented [8,12]. Ten females who had never abused their previous infants were used as controls. Maternal abusive behavior was defined as in [10].

2.2. Procedure

The study was conducted from October 1998 to July 1999. During the mating season, ultrasonography was used to confirm pregnancy and estimate gestational stage in multiparous females who could potentially serve as subjects or controls and had been observed mating in previous weeks. The expected date of parturition was estimated by considering an average gestation length of 168 days or 24 weeks [1].

Starting 6 weeks prior to the estimated date of parturition and through the fourth week of lactation, all subjects and controls were captured once a week (on the same day and at the same time, whenever possible) to obtain blood samples. The animals were trained to run into an indoor capture area, where they were transferred via a transfer box into a standard squeeze cage. One 5-ml blood sample was obtained from the saphenous vein without anesthesia by holding the subject's leg through a hole in the cage. The animal was quickly released into the group after blood sampling. Blood samples were centrifuged and plasma was frozen at $-80°C$ until assayed for 17-β estradiol and progesterone. Behavioral observations of subjects and controls began 8 weeks prior to the estimated date of parturition and continued through the eighth week of lactation. Each subject was focally observed for 1 h/week from an observation tower that allows an unrestricted view of the outdoor compound. All animals were locked out of their indoor housing areas during observation time. Data were collected with a portable computer programmed to allow the recording of frequencies, durations, and sequences of behavior in real time. Behavioral observations included a wide range of social and nonsocial activities (see below). Observation sessions were randomly distributed between 0800 and 1900 h.

Within 24–72 h after they gave birth, all subjects and controls were captured so that their infants could be briefly separated and a microchip be subcutaneously implanted for the purposes of individual recognition. The 10 infants born to control mothers were returned to their biological mothers after the procedure, whereas the infants born to abusive mothers were switched with age-matched infants born to nonabusive females as part of another study. Five abusive mothers adopted a foster infant and five of them rejected it. The five mothers who failed to adopt remained without an infant and data collection with them was terminated (data collection was also terminated with one of the control mothers when she lost her infant at the end of the first month of lactation). Although the cross-fostering procedure could be viewed as a potentially confounding variable within the context of the present study, this is unlikely to be the case because (a) all subjects and controls were handled and briefly separated from their infants with identical procedures and (b) the five abusive mothers who successfully adopted unrelated infants treated these infants as if they were their own offspring [11].

2.3. Behavioral observations

Behavioral data collection focused on social interactions between the focal females and all of the other group members except their own infants. The following interactions were analyzed. Contact = the frequency of contact made and received by focal females. Contact was defined as any bodily contact between two individuals except brief touching or hitting. Grooming = the frequency of grooming bouts initiated and received by focal females. Grooming was defined as picking or brushing the fur of another individual. A contact or grooming bout was considered to have ended after a 10-s interruption. 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. Aggression = the frequency of threats, bites, or slaps initiated and received by the focal females. Infant handling = the frequency of interactions with other females' infants of age 0–12 months, in which the focal females briefly touched, held, carried, or groomed the infant. The frequency of infant handling was corrected for the number of infants present in the group on a weekly basis (number of births per week in the study groups ranged between one and nine). Based on the findings of a previous study, we predicted that abusive mothers would be more socially isolated, more aggressive toward other individuals, and more interested in other females' infants than nonabusive mothers [8].

2.4. Hormonal assays

Hormones were assayed with radioimmunoassay using kits produced by Diagnostic Products (Los Angeles, CA). The estradiol assay had a sensitivity of 5–7 pg/ml with an intra-assay coefficient of variation (CV) of 6% and an interassay CV of 11%. The progesterone assay had a sensitivity of 0.20 ng/ml, with an intra-assay CV of 4% and an interassay CV of 10%.

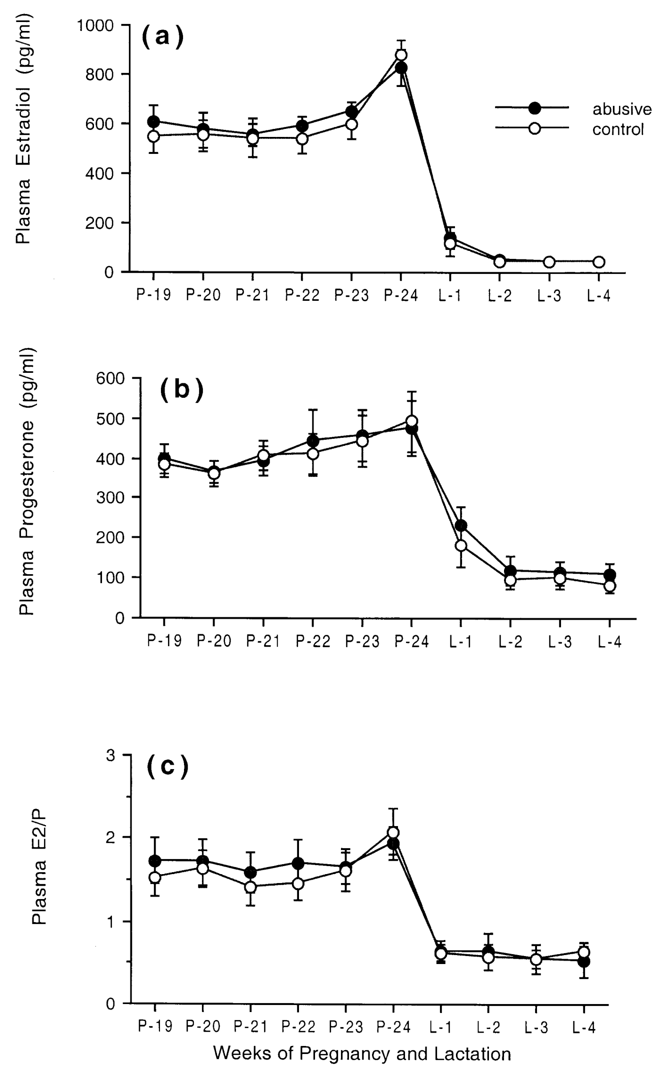

Fig. 1. (a) Mean (± S.E.M.) plasma concentrations of estradiol (pg/ml) per individual during weeks 19–24 of pregnancy and weeks 1–4 of lactation in abusive and control mothers. The weekly changes in estradiol during late pregnancy and early lactation are statistically significant. (b) Mean (± S.E.M.) plasma concentrations of progesterone (pg/ml) per individual during weeks 19–24 of pregnancy and weeks 1–4 of lactation in abusive and control mothers. The weekly changes in progesterone during late pregnancy and early lactation are statistically significant. (c) Mean (± S.E.M.) values of the estradiol-to-progesterone ratio during weeks 19–24 of pregnancy and weeks 1–4 of lactation in abusive and control mothers. The weekly changes in E2/P are statistically significant during late pregnancy but not during early lactation. The number of subjects is 20 during pregnancy and 15 during lactation.

3. Results

Subjects and controls did not differ significantly in terms of their age (mean ± S.E.M., abuse = 10.0 ± 1.0 years; control = 10.4 ± 0.74; $t = -.32$, $df = 18$, ns), number of previous offspring that survived to 1 year of age (abuse = 4.3 ± 0.68; control = 4.0 ± 0.61; $t = .33$, $df = 18$, ns), dominance rank (abuse, high = 4, middle = 4, low = 2; control, high = 2, middle = 2, low = 2; $\chi^2 = 1.07$, $df = 2$, ns), or offspring sex (abuse, male = 5, female = 5; control, male = 4, female = 6; $\chi^2 = 0.65$, $df = 1$, ns).

3.1. Hormonal changes during late pregnancy and early lactation

Repeated measures ANOVA revealed statistically significant changes in the concentrations of plasma estradiol, progesterone, and in the estradiol-to-progesterone ratio during late pregnancy [E2: $F(5,95) = 13.07$, $P < .0001$; P: $F(5,95) = 4.67$, $P < .001$; E2/P: $F(5,95) = 5.31$, $P < .001$] as well as during early lactation, at least for estradiol and progesterone [E2: $F(3,42) = 4.73$, $P < .001$; P: $F(3,42) = 10.41$, $P < .001$; E2/P: $F(3,42) = 0.078$, ns]. Estradiol and progesterone in abusive and control mothers peaked the week before parturition and dropped dramatically in the first and second week of lactation (Fig. 1a,b). The prepartum peak and the postpartum drop in estradiol were more marked than the prepartum peak and the postpartum drop in progesterone. Consequently, the E2/P peaked before parturition and dropped in the first week of lactation (Fig. 1c). Repeated measures ANOVA revealed no significant differences between abusive and control mothers in absolute concentrations of E2, P, or in the E2/P during pregnancy or lactation. Similarly, there were no significant differences between abusive and control mothers in the pattern with which E2, P, or the E2/P changed over time during pregnancy or lactation.

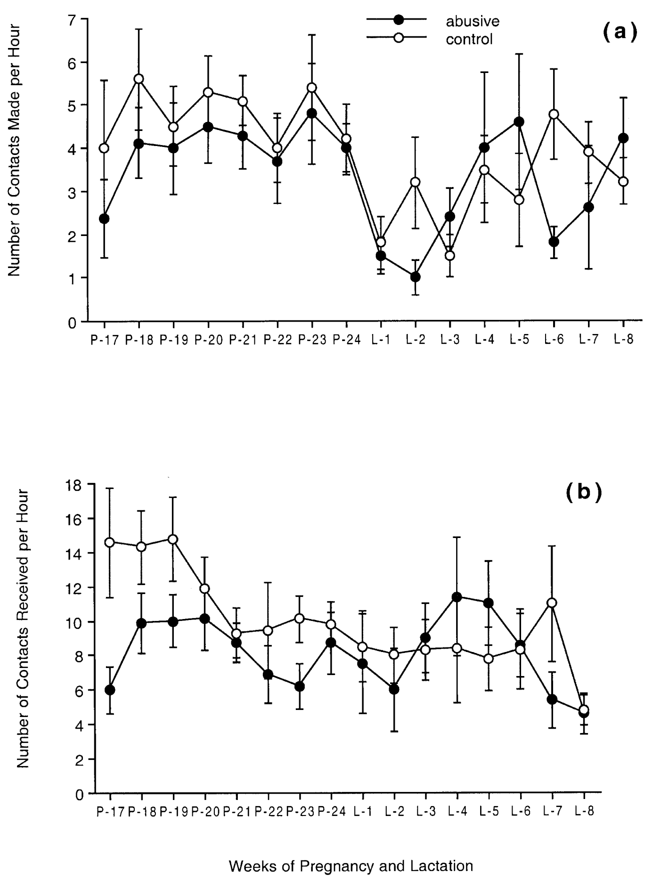

Fig. 2. (a) Mean (± S.E.M.) number of contacts made by mothers with other individuals per hour per individual during weeks 17–24 of pregnancy and weeks 1–8 of lactation in abusive and control mothers. Number of contacts varied significantly during lactation but not during pregnancy. (b) Mean (± S.E.M.) number of contacts received by mothers from other individuals per hour per individual during weeks 17–24 of pregnancy and weeks 1–8 of lactation in abusive and control mothers. Number of contacts varied significantly during pregnancy but not during lactation. The number of subjects is 20 (10 abusive, 10 control) during pregnancy and 15 (5 abusive, 10 control) during lactation.

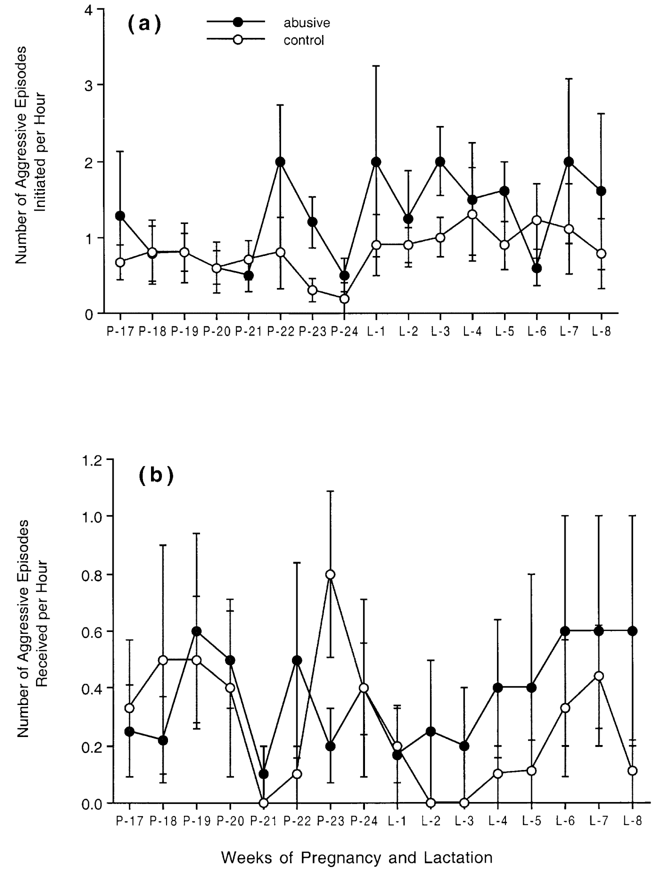

Fig. 3. (a) Mean (± S.E.M.) number of aggressive episodes initiated by mothers per hour per individual during weeks 17–24 of pregnancy and weeks 1–8 of lactation in abusive and control mothers. (b) Mean (± S.E.M.) number of aggressive episodes received by mothers per hour per individual during weeks 17–24 of pregnancy and weeks 1–8 of lactation in abusive and control mothers. The number of subjects is 20 (10 abusive, 10 control) during pregnancy and 15 (5 abusive, 10 control) during lactation.

3.2. Changes in social interactions during late pregnancy and early lactation

Repeated measures ANOVA conducted separately for the last 8 weeks of pregnancy and the first 8 weeks of lactation revealed that the frequency of contact made by abusive and nonabusive mothers did not vary significantly during pregnancy, but dropped dramatically in the first week of lactation and increased thereafter [$F(7,84)=2.17$, $P=.05$; Fig. 2a]. The frequency of contact received decreased significantly over the last 8 weeks of pregnancy [$F(7,126)=2.60$, $P=0.01$], but did not vary significantly during lactation (Fig. 2b). Grooming or aggression involving abusive and nonabusive mothers as actors or recipients did not vary significantly over time during pregnancy or lactation (Figs. 3a,b and 4a,b) although these social interactions were generally infrequent in the first 1–2 weeks of lactation.

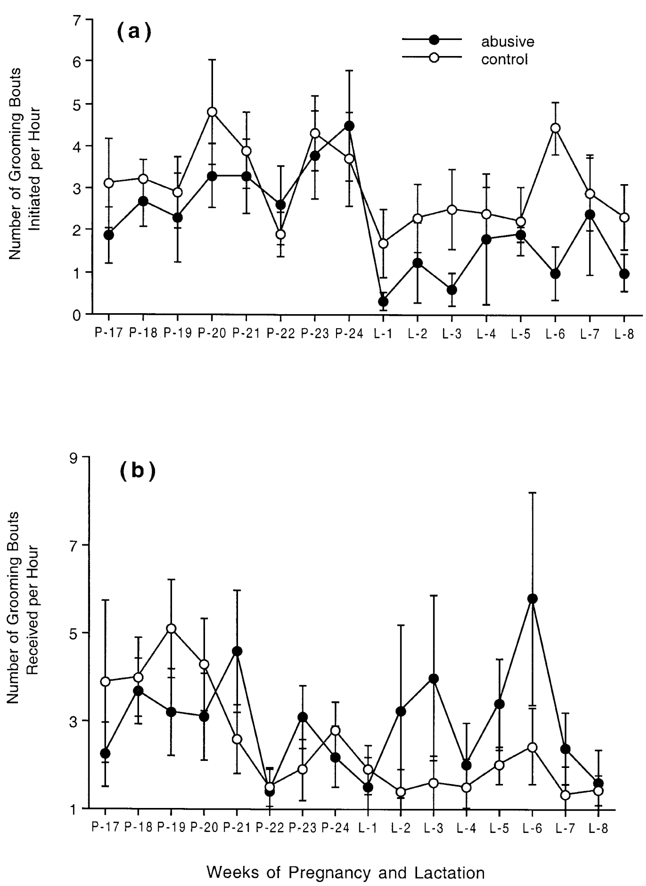

Fig. 4. (a) Mean (±S.E.M.) number of grooming episodes initiated by mothers per hour per individual during weeks 17–24 of pregnancy and weeks 1–8 of lactation in abusive and control mothers. Abusive mothers groomed other individuals less frequently than nonabusive mothers during lactation. (b) Mean (±S.E.M.) number of grooming episodes received by mothers per hour per individual during weeks 17–24 of pregnancy and weeks 1–8 of lactation in abusive and control mothers. The number of subjects is 20 (10 abusive, 10 control) during pregnancy and 15 (5 abusive, 10 control) during lactation.

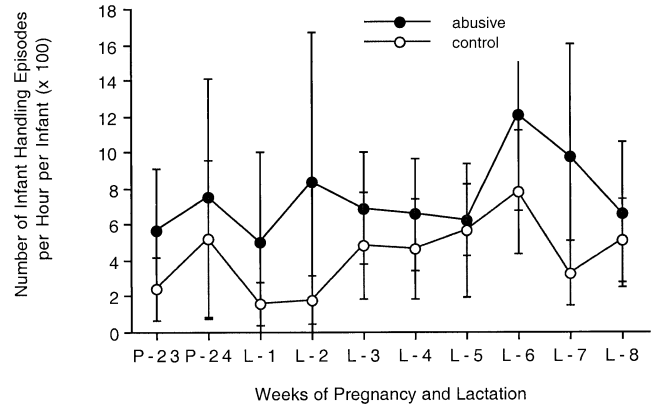

Fig. 5. Mean (±S.E.M.) number of infant handling episodes initiated by mothers per hour per individual during weeks 23–24 of pregnancy and weeks 1–8 of lactation in abusive and control mothers. Infant handling scores were corrected for the number of infants present in the group on a weekly basis by dividing the number of interactions by the number of infants and then multiplying by 100. The number of subjects is 20 (10 abusive, 10 control) during pregnancy and 15 (5 abusive, 10 control) during lactation.

During the last 8 weeks of pregnancy, there were no significant differences between abusive and nonabusive mothers in the frequency of contacts made and received (Fig. 2a,b), grooming done and received (Fig. 3a,b), or aggression done and received (Fig. 4a,b) although abusive mothers received fewer contacts than controls did [$F(1,18)=4.01$, $P<.05$, one-tailed]. During the first 8 weeks of lactation, abusive mothers groomed other individuals less frequently [$F(1,12)=11.64$, $P<.01$]. Abusive mothers generally received more aggression and were groomed more frequently by others than controls did, but differences failed to reach statistical significance. There were no significant differences between abusive and nonabusive mothers for making or receiving contact or for attacking other individuals during lactation. There was no significant interaction between Groups (abusive vs. nonabusive mothers) and Time for any behavioral measure considered during pregnancy or lactation. Thus, the changes in social interactions across pregnancy or lactation were generally similar in abusive and nonabusive mothers.

Pregnancy data on the frequency with which abusive and nonabusive mothers handled other females' infants were only available for the 2 weeks before parturition because most of the subjects gave birth early in the season and therefore, there were no other infants in the group during most of their pregnancy. Thus, the last 2 weeks of pregnancy and the first 8 weeks of lactation were combined in data analysis. The frequency of infant handling did not vary significantly over time and abusive mothers handled other infants more frequently than controls did [$F(1,11)=2.69$, $P=.05$; one-tailed; Fig. 5].

3.3. Behavioral consistency and change in the transition from pregnancy to lactation

To assess whether the social interactions of abusive and nonabusive mothers underwent a significant change from pregnancy to lactation, the behavioral scores for each individual female were averaged across the 8 weeks of pregnancy (2 weeks for infant handling) and the 8 weeks of lactation. There was no significant correlation between pregnancy and lactation for any of the behavioral measures considered. Repeated measures ANOVA revealed statistically significant differences between pregnancy and lactation for making contact with [$F(1,1)=5.29$, $P<.05$], grooming [$F(1,1)=6.91$, $P<.05$], and attacking other individuals [$F(1,1)=7.25$, $P=.01$]. Specifically, making contact with and grooming other individuals were more frequent during pregnancy, whereas aggression was more frequent during lactation. The behavior of abusive and nonabusive mothers was affected by the change in reproductive condition in a different way [contact: $F(1,14)=8.83$, $P=.01$; grooming: $F(1,14)=6.51$, $P<.05$; aggression: $F(1,14)=2.16$, $P=.1$]. The reduction in grooming and increase in aggression associated with lactation were more marked for abusive than nonabusive mothers (Figs. 3a and 4a), whereas the changes in making contact with other individuals were more apparent in the nonabusive mothers (Fig. 2a).

There were no significant differences between pregnancy and lactation in the frequency of infant handling or aggression received by abusive and nonabusive mothers. However, grooming received was affected by the change in reproductive condition [$F(1,14)=6.66$, $P<.05$] and to a different extent for abusive and nonabusive mothers [$F(1,14)=4.74$, $P<.05$]. Specifically, the reduction in grooming received associated with lactation was less marked for abusive mothers than for controls.

Table 1
Mean levels of estradiol (E2) and progesterone (P), and mean values of the estradiol-to-progesterone ratio (E2/P) across pregnancy (PR) and lactation (L) in abusive (Abuse) and nonabusive (Control) mothers. The difference between the mean values of E2, P, and E2/P during pregnancy and lactation (PR-L) is also reported. Hormone levels are reported in picograms per milliliter.

	Abuse (mean ± S.E.M.)	Control (mean ± S.E.M.)
E2 (PR)	635.81 ± 36.09	610.16 ± 49.78
P (PR)	423.10 ± 50.29	416.70 ± 43.83
E2/P (PR)	1.72 ± 0.24	1.62 ± 0.19
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 (PR-L)	521.03 ± 59.63	549.00 ± 56.59
P (PR-L)	257.40 ± 27.88	302.30 ± 28.40
E2/P (PR-L)	0.90 ± 0.17	1.03 ± 0.18

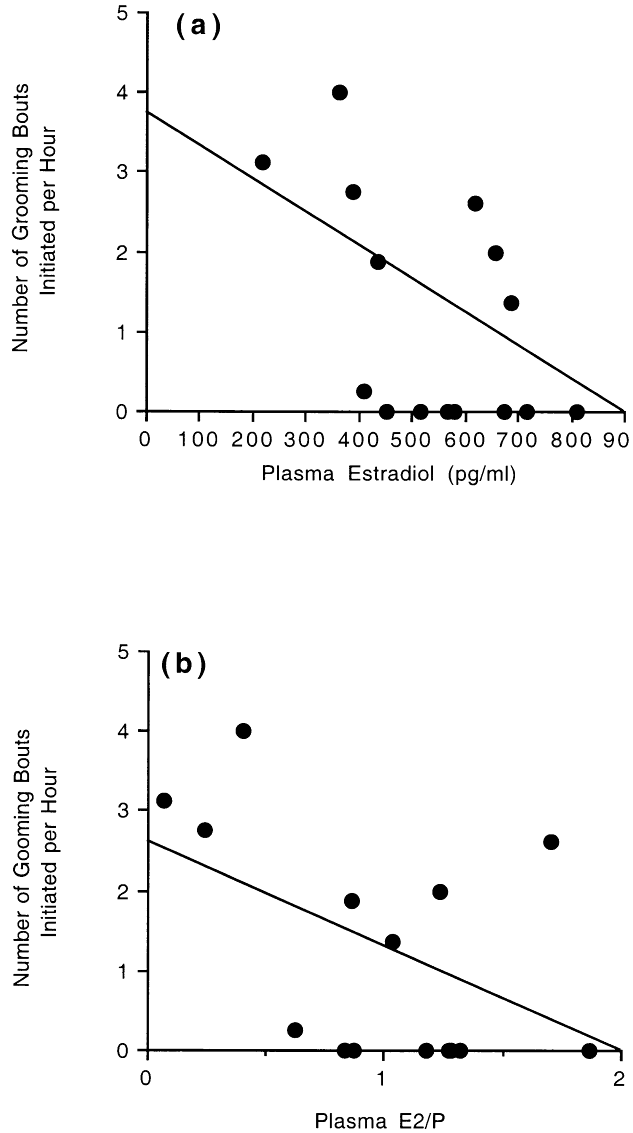

Fig. 6. (a) Correlation between the reduction in estradiol after parturition (values recorded in the last week of pregnancy minus values recorded in the first week of lactation) and the reduction in grooming done by newly lactating females (values recorded in the last week of pregnancy minus values recorded in the first week of lactation). (b) Correlation between the reduction in the estradiol-to-progesterone ratio after parturition and the reduction in grooming done by newly lactating females. The number of subjects is 15 (5 abusive, 10 control).

3.4. Individual differences in hormones and social behavior during pregnancy and lactation

To assess whether hormone levels predicted changes in social interactions during pregnancy or lactation, the scores of E2, P, and the E2/P were averaged across the last 6 weeks of pregnancy and the first 4 weeks of lactation (Table 1). Then correlations between hormonal and behavioral scores were calculated separately for pregnancy and lactation. Since there were no significant differences between abusive and nonabusive mothers in the values of E2, P, and E2/P during pregnancy or lactation, the data from both groups were lumped together to increase the sample size.

During pregnancy, the frequency of aggression done and received was positively correlated with E2 levels (done: $r = .51$, $df = 18$, $P < .05$; received: $r = .44$, $df = 18$, $P = .05$) and the frequency of contacts received was negatively correlated with E2/P ($r = -.49$, $df = 18$, $P < .05$). During lactation, there were no significant correlations between hormones and behavior.

The mean values of E2, P, and E2/P were significantly lower during lactation than during pregnancy (Student's t test for paired samples, E2: $t = 12.99$, $df = 13$, $P < .0001$; P: $t = 13.52$, $df = 13$, $P < .0001$; E2/P: $t = 8.15$, $df = 13$, $P < .0001$; Table 1). To assess whether the magnitude of the reduction in E2, P, and E2/P during lactation predicted the increased frequency of aggression and reduced frequency of contact and grooming among abusive and nonabusive mothers, the mean values of E2, P, E2/P, contact, and grooming during lactation were subtracted from those during pregnancy, whereas the mean values of aggression during pregnancy were subtracted from those during lactation (see Table 1 for hormone levels). Then correlations were calculated between the hormonal and behavioral scores. There were significant negative correlations between reduction in grooming during lactation and reduction in E2 ($r = -.54$, $df = 13$, $P < .05$) and E2/P ($r = -.51$; $df = 13$, $P < .05$; Fig. 6). Thus, among the individual mothers, the greater the reduction in E2 and E2/P during lactation, the smaller the reduction in grooming. Other correlations between hormonal and behavioral variables were not significant.

4. Discussion

The pattern of variation in hormone levels and social interactions across late pregnancy and early lactation was generally similar in abusive and nonabusive mothers. Confirming the findings of previous studies of rhesus macaques and closely related species [2,3,13,19], E2, P, and E2/P peaked the week before parturition and dropped in the first and second weeks of lactation. Grooming or aggression involving abusive and nonabusive mothers as actors or recipients did not vary significantly over time during pregnancy or lactation. Contacts made by mothers were infrequent in the first week of lactation and increased thereafter, whereas contacts received varied significantly during pregnancy but not lactation.

Interestingly, the transition from pregnancy to lactation was associated with a general reduction in making contact with and grooming other individuals, and an increase in aggression. In contrast, other individuals did not appear to treat pregnant and lactating females any differently. These findings are consistent with those of a recent study of pigtail macaques, which reported some changes in female social behavior across pregnancy, but no changes in the way pregnant females were treated by other individuals [9]. Female aggressiveness toward other individuals during lactation is a common phenomenon in most mammals including primates [6], although previous studies of maternal aggression in primates did not compare female aggressive behavior during pregnancy and lactation [7,17].

Quantitative differences between abusive and nonabusive mothers in the measures of contact and grooming received, aggression, and infant handling were in the same direction as those reported in a previous study [8], although in some cases, they did not reach statistical significance. The lack of correlation between the behavioral scores of pregnancy and lactation across individuals suggests that individuals were affected by motherhood in different ways. Most notably, the reduction in active grooming and increase in aggression associated with lactation were more marked for abusive than nonabusive mothers. Since there were no significant differences in hormone levels between abusive and nonabusive mothers, it may be argued that for abusive individuals, the presence of infants was associated with a general decrease in friendliness toward other group members. Alternatively, it is possible that differences in behavior between abusive and nonabusive mothers are associated with differences in hormones or neurotransmitters not considered in this study (e.g., prolactin, oxytocin, cortisol, or β-endorphin; [4]). It is also possible that the adoption of unrelated infants by abusive mothers may have confounded the behavioral comparisons between subjects and controls during lactation. However, the confounding effect of the infant cross-fostering procedure is likely to have been minimal for the following reasons: (a) when rhesus mothers successfully adopt alien infants, their subsequent behavior is generally not affected by the procedure [11,16]; and (b) the few differences in social behavior between abusive and nonabusive mothers reported in this study are entirely consistent with those reported in a previous study in which all mothers were observed with their own offspring [8].

When the relation between hormones and social behavior was investigated by combining data from all individuals, some significant correlations emerged. During pregnancy, the frequency of aggression done and received was positively correlated with E2 levels, whereas the frequency of contacts received was negatively correlated with E2/P. Furthermore, the reduction in E2 and E2/P after parturition was inversely related with the reduction in grooming behavior during lactation. Specifically, among the individual mothers, the greater the reduction in E2 and E2/P during lactation, the smaller the reduction in grooming. There was no significant correlation, however, between absolute hormone levels during lactation and individual differences in social behavior.

Correlations between E2 and grooming or aggression have also been reported during the menstrual cycle or pregnancy in macaques [9,15]. Correlational data, of course, do not provide evidence of cause–effect relations between hormones and behavior or information on the mechanisms through which hormones may affect grooming or aggression. There is evidence, however, that estrogen alters the functionality of neurotransmitters such as noradrenaline and serotonin, which are known to play a role in the regulation of aggressive behavior [14]. Therefore, it is possible that the correlation between E2 and aggression levels during pregnancy reflects interindividual differences in estrogen-mediated modulation of neurotransmission. Although these findings are clearly preliminary and their interpretation speculative, preliminary evidence that interindividual variability in female social behavior, at least during pregnancy, is accounted for by endocrine variables can encourage further primate studies of hormones and social behavior in which endocrine variables can be experimentally manipulated [13].

In sum, this study provided the first comprehensive investigation of periparturitional changes in hormones and social behavior in female primates. Moreover, it provided, for the first time, hormonal data concerning macaque mothers who physically abuse their infants. Thus, the information presented here contributes to our knowledge of basic endocrine and behavioral processes associated with pregnancy, parturition, and lactation in macaques. Taken together, the findings of this study suggest that the changes in social behavior associated with the transition from pregnancy to lactation are more marked than those, if any, occurring across the last weeks of pregnancy and the early weeks of lactation.

Acknowledgments

We thank Jessica Ganas for assistance with the animal handling procedures. This research was supported by NIMH grants R01-MH57249 and R01-MH62577, and in part by NIH grant RR-00165 to the Yerkes Regional Primate Research Center. All hormonal assays were performed by the Yerkes Assay Services. The Yerkes Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care.

References

[1] Ardito G. Checklist of the data on the gestation length of primates. J Hum Evol 1976;5:213–22.

[2] Bosu WTK, Johansson EDB, Gemzell C. Patterns of circulating oestrone, oestradiol-17 β and progesterone during pregnancy in the rhesus monkey. Acta Endocrinol 1973;74:743–55.

[3] Hodgen GD, Dufau ML, Catt KJ, Tullner WW. Estrogens, progesterone and chorionic gonadotrophin in pregnant rhesus monkeys. Endocrinology 1972;91:896–900.

[4] Keverne EB. Primate social relationships: their determinants and consequences. Adv Study Behav 1992;21:1–37.

[5] Lindburg DG. Ecological requirements of macaques. Lab Anim Sci 1991;41:315–22.

[6] Maestripieri D. Functional aspects of maternal aggression in mammals. Can J Zool 1992;70:1069–77.

[7] Maestripieri D. Costs and benefits of maternal aggression in lactating female rhesus macaques. Primates 1994;35:443–53.

[8] Maestripieri D. Parenting styles of abusive mothers in group-living rhesus macaques. Anim Behav 1998;55:1–11.

[9] Maestripieri D. Changes in social behavior and its hormonal correlates across pregnancy in pig-tailed macaques. Int J Primatol 1999;20:707–18.

[10] Maestripieri D, Megna NL. Hormones and behavior in abusive and nonabusive rhesus macaque mothers: 2. Mother–infant interactions. Physiol Behav 2000;71:37–43.

[11] Maestripieri D, Megna NL, Jovanovic T. Adoption and maltreatment of foster infants by rhesus macaque abusive mothers. Dev Sci 2000;3:287–93.

[12] Maestripieri D, Tomaszycki M, Carroll KA. Consistency and change in the behavior of rhesus macaque abusive mothers with successive infants. Dev Psychobiol 1999;34:29–35.

[13] Maestripieri D, Zehr JL. Maternal responsiveness increases during pregnancy and after estrogen treatment in macaques. Horm Behav 1998;34:223–30.

[14] McEwen BS, Alves SE. Estrogen actions in the central nervous system. Endocr Rev 1999;20:279–307.

[15] Michael RP, Herbert J, Welegalla J. Ovarian hormones and grooming behaviour in the rhesus monkey (*Macaca mulatta*) under laboratory conditions. J Endocrinol 1966;36:263–79.

[16] Smith S. Infant cross-fostering in rhesus monkeys (*Macaca mulatta*): a procedure for the long-term management of captive populations. Am J Primatol 1986;11:229–37.

[17] Troisi A, D'Amato FR, Carnera A, Trinca L. Maternal aggression by lactating group-living Japanese macaque females. Horm Behav 1988;22:444–52.

[18] Wallen K, Tannenbaum PL. Hormonal mediation of sexual behavior and affiliation in rhesus monkeys. Ann N Y Acad Sci 1997;807:185–202.

[19] Walsh SW, Wolf RC, Meyer RK, Robinson JA. Estrogens in the utero-ovarian, uterine, and peripheral plasma in pregnant rhesus monkeys. Biol Reprod 1979;20:606–10.