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# Maternal Responsiveness Increases during Pregnancy and after Estrogen Treatment in Macaques

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**Maternal responsiveness in primates has long been considered emancipated from endocrine factors and entirely dependent on experience and cognition. Here we report that group-living pigtail macaque females increased their rate of interaction with infants in the last weeks of pregnancy in correspondence with an increase in plasma levels of estradiol and progesterone. Estrogen treatment increased the rate at which ovariectomized rhesus females interacted with infants. This is the first evidence that steroid hormones influence maternal responsiveness in anthropoid primates. All untreated ovariectomized females and nonpregnant females interacted with infants, indicating that although estrogen can enhance responsiveness to infants, ovarian or pregnancy hormones are not necessary for the expression of infant-directed behavior in female macaques. The findings of this study suggest fundamental similarities, rather than differences, in the endocrine modulation of maternal responsiveness in primates and other mammals.** 

In human and nonhuman primates, maternal responsiveness has often been viewed as emancipated from neuroendocrine modulation and entirely dependent on experiential, cognitive, and social factors (Benedek, 1970; Coe, 1990; Sternglanz and Nash, 1991; Keverne, 1996; see Maestripieri, in press, for a review). This view implies a fundamental difference in the regulation of maternal behavior between primates and other mammals, where maternal responsiveness is affected by the endocrine changes underlying pregnancy and lactation. For example, in rats and sheep, female responsiveness to young increases dramatically during late pregnancy and is associated with an increase in circulating estradiol and in the estradiol to progesterone ratio (Rosenblatt, Mayer, and Giordano, 1988; Poindron and Levy, 1990). In rats, however, maternal responsiveness can also be elicited in virgin females through repeated exposure to pups (Rosenblatt, 1967) and sensory stimuli from the pups are sufficient to maintain maternal behavior during lactation (Stern, 1989). Thus, in nonprimate mammals, pregnancy and lactation hormones enhance maternal responsiveness and behavior although they are not strictly necessary for their onset or maintenance (Stern, 1989).

Although social and experiential variables have an important influence on maternal behavior in nonhuman primates (Pryce, 1996), a number of recent studies have provided evidence that maternal responsiveness is not completely emancipated from endocrine influence. In New World monkeys such as red-bellied tamarins (*Saguinus labiatus*) and common marmosets (*Callithrix jacchus*), there is evidence that hormones influence both responsiveness to young during pregnancy and quality of maternal care during lactation (Pryce, Abbott, Hodges, and Martin, 1988; Pryce, Döbeli, and Martin, 1993). In Old World monkeys such as rhesus macaques (*Macaca mulatta*), earlier studies using individually housed animals failed to detect changes in female responsiveness to infants in relation to pregnancy or endocrine status (Holman and Goy, 1980; Gibber, 1986). A recent study of group-living pigtail macaques (*Macaca nemestrina*), however, reported that female interest in other females' infants increased during middle-late pregnancy (Maestripieri and Wallen, 1995). In chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*), preliminary data suggest

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that hormone concentrations during pregnancy predict maternal competence during early lactation (Dahl, Bard, Jones, and Gould, 1994; Bahr, 1995). Similarly, a recent study in humans showed that the pattern of change in the ratio of estradiol to progesterone in late pregnancy was related to postpartum feelings of attachment to the newborn (Fleming, Ruble, Krieger, and Wong, 1997). To date, however, there is no evidence that steroid hormone administration enhances maternal responsiveness in anthropoid primates (i.e., Old World monkeys and apes) or humans.

This research investigated the influence of pregnancy and steroid hormones on maternal responsiveness in group-living pigtail and rhesus macaques. In the study of pigtail macaques, we tested the hypothesis that the hormonal changes occurring during pregnancy, and in particular the increase in circulating estradiol, would enhance female interest in infants. Pigtail macaques are suitable subjects for a longitudinal study of pregnancy because they are nonseasonal breeders and adult females have the opportunity to interact with other females' infants throughout their pregnancy. In the study of rhesus macaques, we tested the hypothesis that treating ovariectomized females with estrogen would increase their interest in infants. This study was conducted during the first 3 months of the rhesus birth season and nonpregnant intact females were used as controls.

## METHODS

### Experiment 1: Maternal Responsiveness during Pregnancy in Pigtail Macaques

***Subjects and housing.*** Study subjects were 8 pigtail macaque females living in a social group composed of 3 adult males, 31 adult females, and their immature offspring. The group was housed in a 25 × 25-m outdoor compound with attached indoor enclosure at the Field Station of the Yerkes Regional Primate Research Center of Emory University in Lawrenceville, Georgia. Subjects ranged in age from 5 to 12 years and were all multiparous having delivered at least one offspring prior to this study. Monkeys were fed twice daily and water was continuously available. The dominance ranks of all adult females in the group were assessed with data on aggression, submission, and displacements collected prior to onset of the study. The dominance hierarchy was linear and did not change during the course of the study.

***Procedures.*** The study was conducted from October 1996 to July 1997. Ultrasonography was used to detect pregnancy and estimate gestational stage in multiparous females who had been observed mating in previous weeks or looked pregnant. Two females were recruited into the study before conception. The other six females were recruited when pregnancy was verified with ultrasonography. One female was recruited at Pregnancy Week 3, three at Week 5, one at Week 8, and one at Week 15. All eight subjects were followed until they gave birth or had a miscarriage (two cases, one in the third and one in the fifth month of pregnancy). For the six females who gave birth, the exact gestational stage at the time of recruitment was confirmed retrospectively from the date of parturition, considering an average gestation length of 24 weeks (Ardito, 1976).

On the same day and time each week, all subjects were captured to obtain blood samples. Subjects were trained to run into an indoor capture area, where they were transferred via a transfer box into a standard squeeze cage. One 3-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-ß estradiol and progesterone.

Each week, all subjects were focally observed for 1 h from an observation tower which allows an unrestricted view of the outdoor compound. 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. Maternal responsiveness was operationally defined as female interest in infants and measured with the frequency with which the focal subjects initiated interactions with other females' infants (age 0–3 months). Interactions with infants were collectively referred to as infant handling and included behaviors such as brief touching, grooming, carrying, or harassment (pulling, dragging, or hitting). Although infant harassment was relatively infrequent (the most common form of infant handling was brief touching), it was included in the analysis because, similar to benign infant handling, it reflects interest in infants (see Maestripieri and Wallen, 1995). Infant handling scores were corrected for infant availability by dividing the frequency of handling each week by the number of infants present in the group in that week. During the study period, the number of infants of age

0–3 months present in the group in a given week ranged from 2 to 13.

***Hormonal assays.*** Hormones were assayed with radioimmunoassay using kits produced by Diagnostic Products Corp. (Los Angeles, CA). The estradiol assay had a sensitivity of 5–7 pg/ml with an intraassay 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 intraassay CV of 4% and an interassay CV of 10%.

### Experiment 2: Effects of Estrogen Treatment on Maternal Responsiveness in Ovariectomized Female Rhesus Macaques

***Subjects and housing.*** Study subjects were 5 ovariectomized and 6 nonpregnant rhesus macaque females living in a social group composed of 3 adult males, 46 adult females, and their immature offspring. The group was housed in a 30 $\times$ 30-m outdoor-indoor compound under conditions similar to those of the pigtail macaques. All intact females were multiparous and varied in age from 6 to 15 years. All ovariectomized females underwent bilateral ovariectomy at 1 year of age and were 16 years old at the time of the study. They had been previously used in studies involving estrogen treatments but had not participated in any such studies for at least 1 year prior to the present research. The female dominance hierarchy was linear and did not change during the course of the study. Nonpregnant and ovariectomized females did not differ significantly in their dominance rank.

***Procedures.*** The study was conducted during the rhesus birth season, from April to July 1997. As soon as the first three infants were born in the group, all multiparous females were screened for pregnancy with ultrasonography. Six nonpregnant females were recruited as subjects along with the five ovariectomized females. The nonpregnant females were healthy and reproductively active individuals who gave birth late in the previous season. The five ovariectomized females were treated with estrogen during either the first 6 weeks ($N = 2$) or the second 6 weeks of the study ($N = 3$). Treatments were made using 4.5-cm Silastic capsules containing crystalline 17-ß estradiol, which were subcutaneously implanted between the subject's shoulders. Weekly blood samples and focal behavioral observations were conducted each week with procedures similar to those used with the pigtail macaques. Nonpregnant and ovariectomized females were followed for 12 weeks and behavioral data were analyzed with procedures similar to those used for the pigtail macaques. Weekly rates of infant handling were corrected for the number of infants (age 0–3 months) present in the group, which ranged from 3 to 23. Hormonal assay procedures were similar to those used for the pigtail macaques.

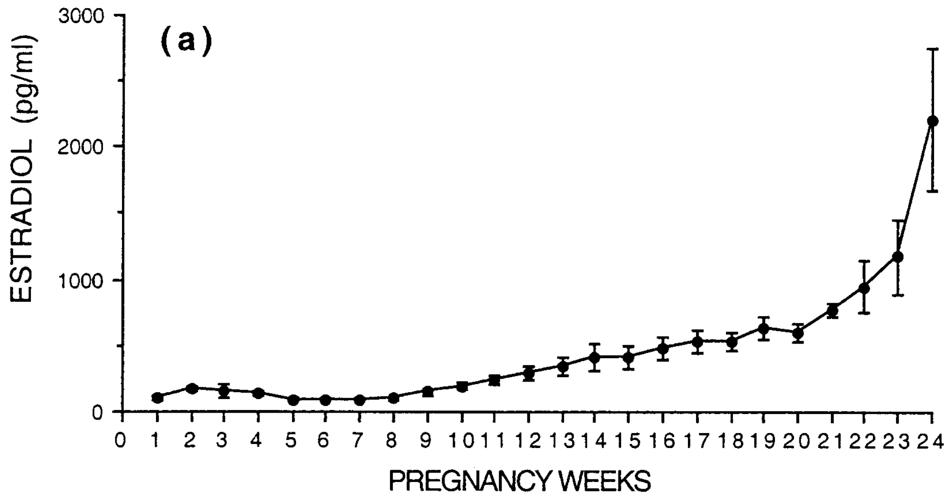
## RESULTS

### Experiment 1

Estradiol increased gradually during pregnancy, peaking the last week before parturition (Fig. 1a). Progesterone peaked during pregnancy Weeks 7–10, decreased, and then increased again over the last 5 weeks of pregnancy (Fig. 1b). For analysis purposes, pregnancy was divided into three 8-week periods. Repeated measures ANOVA revealed a significant difference in the infant-handling rate among the three periods [$F(2,5) = 6.67$, $P < 0.05$], with infant-handling rate being significantly higher in the third than in the first period (Bonferroni-Dunn post hoc test, $P < 0.05$; Fig. 2a). Regression analyses indicated that there was no significant association between infant-handling rate and pregnancy progression in the first 8-week period [$r = 0.49$, $F(1,6) = 1.99$, ns] or in the second period [$r = 0.70$, $F(1,6) = 5.76$, ns]. In the third 8-week period, however, the infant-handling rate increased significantly as pregnancy progressed [$r = 0.87$, $F(1,6) = 19.67$, $P < 0.01$]. The mean rate of infant handling in the last 8 weeks of pregnancy was significantly predicted by levels of circulating estradiol [$r = 0.81$, $F(1,6) = 11.73$, $P < 0.05$] and especially by changes in the estradiol to progesterone ratio [$r = 0.84$, $F(1,6) = 14.90$, $P < 0.01$; Fig. 2b] but not by progesterone [$r = 0.69$, $F(1,6) = 5.54$, $P < 0.1$]. The average rate of infant handling throughout pregnancy tended to be higher the higher the dominance rank of the subjects [$r = 0.61$, $F(1,6) = 3.53$, $P = 0.1$]. The tendency for infant-handling rate to increase during late pregnancy, however, was observed for all subjects, irrespective of their dominance rank.

### Experiment 2

The plasma levels of estradiol and progesterone in untreated ovariectomized females and nonpregnant females remained low throughout the study period (Table 1). One nonpregnant female had a peak in estradiol followed by one in progesterone in the sec-



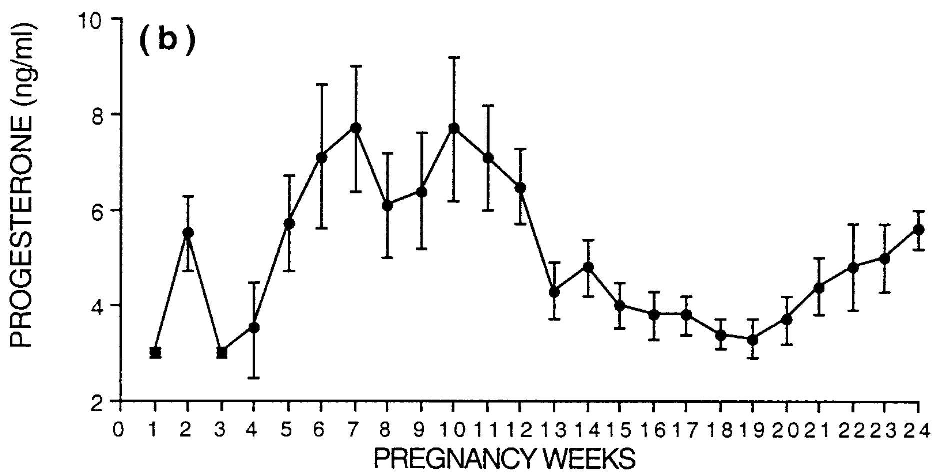




**FIG. 1.** (a) Mean (± SEM) plasma concentrations of estradiol per individual per week during pregnancy in pigtail macaques. (b) Mean (± SEM) plasma concentrations of progesterone per individual per week during pregnancy in pigtail macaques. Sample sizes: weeks 0–2 = 2; 3–5 = 3; 5–8 = 6; 8–11 = 7; 11–15 = 6; 15–21 = 7; 21–24 = 6.

ond week of the study period, suggesting the occurrence of ovulation. The treatment of ovariectomized females resulted in plasma estradiol concentrations of about 250 pg/mg, which remained constant during the 6-week treatment. The progesterone levels of ovariectomized females remained low during the period of the estrogen treatment.

The ovariectomized females showed significantly higher infant handling rates with the estrogen treatment than without treatment (t test for paired samples, $t = 4.76$, $df = 4$, $P < 0.01$; Fig. 3; in most cases, the increase in infant handling was already apparent in the first week of treatment and was reduced in the first week following the estrogen capsule removal). The estrogen-treated ovariectomized females also tended to show higher infant-handling rates than nonpregnant females (t test for unpaired samples, $t = 2.09$, $df = 9$, $P = 0.06$; Fig 3), while the infant handling rates of nonpregnant and untreated ovariectomized females were not significantly different ($t = 1.17$, $df = 9$, ns; Fig.

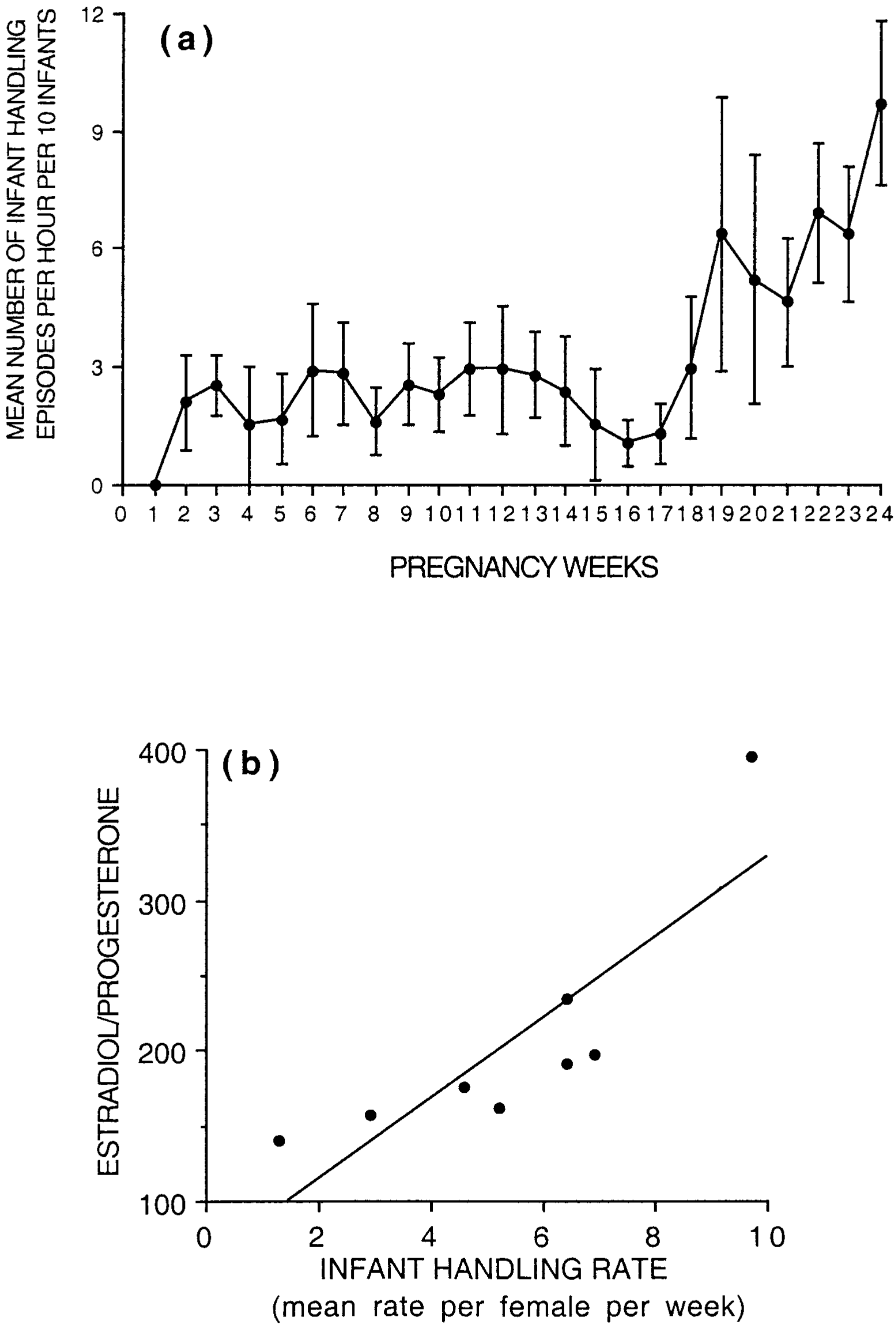



**FIG. 2.** (a) Mean (± SEM) rates of infant handling per hour per individual during pregnancy in pigtail macaques. Infant-handling rates are calculated as the number of infant-handling episodes per 10 infants present in the group. (b) Linear regression of estradiol to progesterone ratio and infant handling rate (mean infant-handling rate per female per week) during the last 8 weeks of pregnancy in pigtail macaques.

3). The effects of estradiol on infant handling by ovariectomized females appeared to be independent from prolactin because we found no association between prolactin levels and infant handling in treated and untreated ovariectomized females (unpublished results). Dominance rank was not significantly related to the infant-handling rates of nonpregnant and untreated ovariectomized females [$r = 0.19$, $F(1,10) = 0.34$, ns].

**TABLE 1**
Hormonal Levels in Estrogen-Treated and Untreated Ovariectomized Females and in Nonpregnant Females

| Hormone | Ovex with E (mean ± SEM) | Ovex without E (mean ± SEM) | Nonpregnant females (mean ± SEM) |
|---|---|---|---|
| Estrogen (pg/ml) | 252.3 ± 38.2 | <10; below assay resolution | 34.2 ± 3.0 |
| Progesterone (ng/ml) | 0.65 ± 0.09 | 0.63 ± 0.11 | 1.05 ± 0.13 |

## DISCUSSION

This study documented the changes in estradiol and progesterone during pregnancy in pigtail macaques and provided both correlational and experimental evidence for the role of hormones in modulating maternal responsiveness in macaques.

In pigtail macaques, plasma estradiol levels increased during late pregnancy, with a final peak in the last 3 weeks before parturition. Plasma progesterone levels increased in early pregnancy, decreased in mid-pregnancy, and increased again in the last weeks before parturition. These findings are in agreement with those of previous studies (pigtail macaques: Chandrashekar, Wolf, Dierschke, Sholl, Bridson, and Clark, 1980; Chandrashekar, Diersche, and Wolf, 1987; rhesus macaques: Hodgen, Dufau, Catt, and Tullner, 1972; Bosu, Johansson, and Gemzell, 1973; Bielert, Czaja, Eisele, Scheffler, Robinson, and Goy, 1976; Walsh, Wolf, Meyer, and Robinson, 1979) and indicate that, unlike nonprimate mammals and some New World monkeys, in macaques late pregnancy is characterized by an increase rather than a decrease in progesterone. Similar to other mammals, however, the estradiol to progesterone ratio increases during macaque late pregnancy because the increase in plasma levels of estradiol is greater than that of progesterone.

In rhesus macaques, nonpregnant females had low levels of circulating estradiol and progesterone, and with the exception of one female at the beginning of the birth season, they did not show the changes in plasma estradiol and progesterone characteristic of ovulation. This finding confirms previous reports showing that ovulation is seasonal in rhesus macaques and suppressed during the birth season (e.g., Walker, Wilson, and Gordon, 1984). The ovariectomized rhesus females had negligible plasma estradiol, and their plasma levels of progesterone were similar to those of nonpregnant females. The treatment of ovariectomized females with estrogen resulted in plasma estradiol levels higher than those of

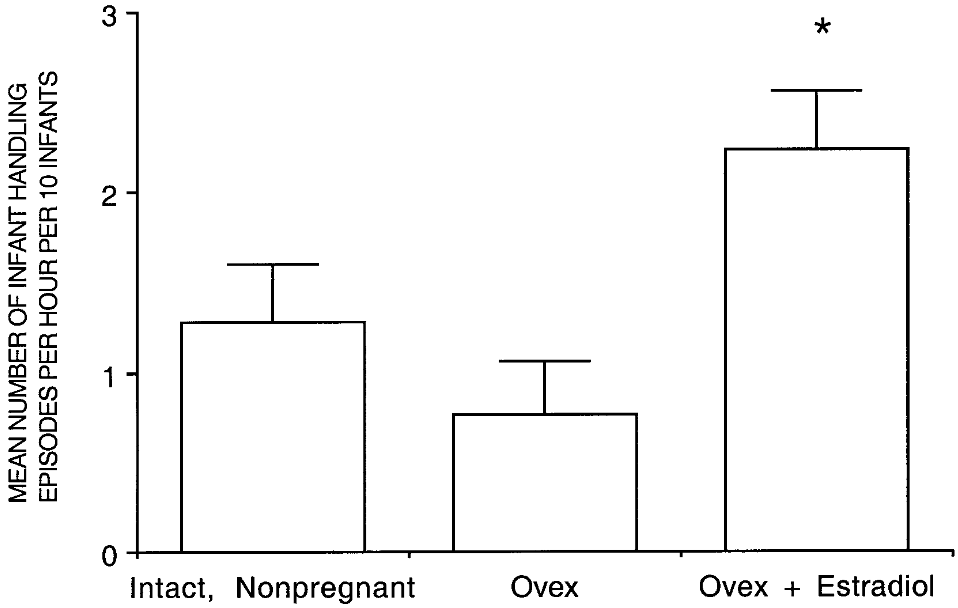



**FIG. 3.** Mean (+ SEM) rates of infant handling per hour per individual in intact nonpregnant, untreated ovariectomized (Ovex), and estrogen-treated ovariectomized (Ovex + Estradiol) rhesus females. Infant-handling rates are calculated as the number of infant-handling episodes per 10 infants present in the group. *$P < 0.01$ (see Results).

nonpregnant females and comparable to those normally observed in early-middle pregnancy (Bosu *et al.*, 1973).

In pigtail macaques, the rate at which females initiated interactions with other females' infants increased in late pregnancy and peaked the week before parturition. In a previous study of pigtail macaques, we reported that female infant handling peaked in middle-late pregnancy and decreased around the time of parturition (Maestripieri and Wallen, 1995). The reason for this discrepancy is unclear but it may be due to methodological differences, as in the first study we obtained data on female infant handling from focal observations of infants, whereas in the present study we focally observed the pregnant females.

Although the peak in infant handling rate coincided with the peak of estradiol the week before parturition, the changes in infant-handling rates during the last 8 weeks of pregnancy were also significantly associated with changes in the estradiol to progesterone ratio. This finding suggests that although female interest in infants is primarily affected by estradiol, the effect of estradiol may be modulated by progesterone. A similar conclusion has been drawn from studies of rats and marmosets (Rosenblatt *et al.*, 1988; Pryce *et al.*, 1993).

Among rhesus macaques, infant handling was shown by all nonpregnant and untreated ovariectomized females, indicating that pregnancy or ovarian hormones are not necessary for the expression of female interest in infants in macaques. In fact, at 1 year of age, and therefore long before puberty, rhesus females are already more interested in infants than males (Lovejoy and Wallen, 1988; Wallen, Maestripieri, and Mann, 1995), suggesting that this sex difference may be due to genetic or prenatal endocrine factors. The increase in infant handling often reported for primate females during adolescence (Maestripieri, 1994a), however, may be associated with the hormonal changes occurring at this age.

The 6-week treatment with estradiol dramatically increased the rate of infant handling by ovariectomized females. This finding represents the first evidence that the administration of steroid hormones enhances maternal responsiveness in anthropoid primates. This result also further supports the hypothesis that the pregnancy-related changes in female infant handling observed in pigtail macaques are mainly driven by estradiol. The rate of infant handling shown by estrogen-treated ovariectomized females also tended to be higher than the average rate of infant handling shown by nonpregnant females.

In pigtail macaques, infant-handling rates tended to be higher the higher the dominance rank, confirming a finding already reported in a previous study (Maestripieri and Wallen, 1995). This rank effect can be explained by the risk of maternal aggression incurred by low ranking females when handling higher ranking females' infants (Maestripieri, 1994b). In rhesus macaques, however, dominance rank was not a good predictor of differences in infant-handling rates among nonpregnant and untreated ovariectomized females.

In pigtail macaques, all pregnant females were multiparous whereas all the ovariectomized rhesus females were nulliparous. It is conceivable to hypothesize that the increase in infant-handling rate during late pregnancy might be even more apparent in nulliparous than in multiparous females because maternal experience might reduce the influence of hormonal changes on responsiveness to infants. Ultimately, however, this hypothesis needs to be tested in future studies, along with the hypothesis that estrogen administration increases responsiveness to infants among multiparous as well as nulliparous females.

Female interest in infants may be influenced by variables other than hormones, dominance rank, or parity. There is some evidence that part of the attractiveness of infants to older females results from a novelty effect. For example, in seasonal macaque species, infants born early in the season usually receive more attention than infants born late in the season, when many infants are already present in the group (Maestripieri, 1994c). This novelty effect may explain why, in the present study, the rates of infant handling among pigtail macaques were, on average, 10 times higher than among rhesus macaques. In rhesus macaques there were, on average, 10 times more infants available for handling than in pigtail macaques and, although infant-handling rates were corrected for availability of infants in both species, the difference in infant-handling may have reflected the fact that young infants were relative rare in one species and much more common in the other. The species difference in infant-handling rate may also have reflected a density effect: if females have limited time to interact with infants, the number of interactions per infant will decrease as the number of infants increases, thus explaining why infant-handling rates per infant are lower among rhesus than among pigtail macaques.

In summary, the findings of this study indicate that, although hormones are not necessary for maternal responsiveness to occur in macaques, pregnancy hormones and exogenous estradiol can enhance responsiveness to infants even in maternally experienced females. Therefore, the findings of this study indicate that maternal responsiveness in primates is not completely emancipated from hormones and that there is a fundamental continuity in the endocrine modulation of maternal responsiveness in primates and other mammals.

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