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TEMPORAL AND SOCIAL FACTORS INFLUENCING BEHAVIORAL AND HORMONAL RESPONSES TO SEPARATION IN MOTHER AND INFANT SQUIRREL MONKEYS

SEYMOUR LEVINE,[1] SANDRA G. WIENER,[1] and CHRISTOPHER L. COE[2]
[1]Department of Psychiatry and Behavioral Sciences, Stanford University School of Medicine, Stanford, California, U.S.A. and [2]Harlow Primate Laboratory, Department of Psychology, University of Wisconsin, Madison, Wisconsin, U.S.A.

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SUMMARY

The behavioral and hormonal responses of mother and infant squirrel monkeys (*Saimiri sciureus*) were examined to assess temporal and environmental factors that influence the response to separation. In two experiments evaluating the effects of 1-, 3-, 6-, and 24-hr separations, it was found that signs of infant behavioral agitation decreased over time, whereas adrenocortical activation persisted or even increased. Moreover, two separation environments were shown to differentially affect behavioral and hormonal responses. Separated infants vocalized significantly more when their mothers were proximal than when isolated, but showed lower cortisol levels in the adjacent separation than in the total-isolation condition. These data indicate that the intensity of the infant's calling response cannot be used to predict internal state (as reflected by cortisol levels). Furthermore, vocalization rate is highly dependent upon contingent stimuli, such as the presence of maternal cues. Following separation, the mothers also showed elevated cortisol levels. However, both the magnitude and pattern of the response differed considerably from that of the infant.

INTRODUCTION

TO A LARGE extent studies on mother-infant relationships in nonhuman primates have employed separation paradigms to examine the infant's behavioral and physiological responses following loss of the mother. Based on available evidence, it has become increasingly apparent that the biobehavioral responses to disruptions in the mother–infant relationship are dependent upon the environmental conditions in which separation occurs (Coe *et al.*, 1983b; Mineka & Suomi, 1978; Rosenblum & Plimpton, 1981; Levine *et al.*, 1985; Bayart *et al.*, 1990; Wiener *et al.*, 1990). Specifically, two variables appear to be of significance in modulating the infant's response to maternal loss: the presence of familiar social partners and the availability of maternal cues. The former generally reduce both vocalizations and hypothalamic–pituitary–adrenal (HPA) activity. The presence of

Address correspondence and reprint requests to: Dr. Seymour Levine, Laboratory of Developmental Psychobiology (Bldg. 7-930T), Department of Psychiatry and Behavioral Sciences, Stanford University School of Medicine, Stanford University, Stanford, CA 94305-5095.

maternal cues, in contrast, typically elevates vocalizations and suppresses the response of the HPA system.

This inverse relationship between vocalization and HPA activity has been observed in several studies (Wiener *et al.*, 1988) and has led to an alternative view of the significance of separation-induced vocalization. The original descriptions of the behavioral responses following separation characterized the infant's initial responses, particularly the vocalizations, as a stage of protest. In contrast, we have hypothesized (Levine, 1983) that the infant's immediate responses are important because they reflect active attempts to cope with the loss of the mother. Furthermore, as others have also suggested, these behaviors may represent an adaptive response for reestablishing contact with the mother (Rosenblum & Plimpton, 1981). In addition, one might hypothesize from a coping perpective that expression of this behavioral response may reduce the biological cost of the high levels of glucocorticoids induced by the separation (Munck *et al.*, 1984; Levine & Ursin, 1991). This prediction is directly opposite from the one anticipated if calling were simply an expression of distress and protest.

In a recent series of studies (Bayart *et al.*, 1990; Wiener *et al.*, 1990) the inverse relationship between vocalization and levels of plasma cortisol following separation was observed when infants were separated in the visual presence of the mother (i.e., "adjacent separation"). When compared to totally isolated infants, the infants that were adjacent to their mother emitted significantly more separation-induced vocalizations. The totally isolated infants produced fewer calls initially, and at the end of a 24-hr separation were barely vocalizing. However, at the end of the 24-hr period the totally separated infants had significantly higher levels of plasma cortisol, reflecting increased HPA activity.

The present experiments were undertaken to examine in greater detail the relationship between vocalization and the endocrine response to adjacent separation. In the first study, vocalization and activity were measured 1, 3, and 6 hr following adjacent separation. In contrast to the study by Wiener *et al.* (1990), blood samples were obtained at the same time as the behavioral measures. This enabled us to closely examine the relationship between the behavioral and physiological responses.

Most of the studies that have used separation to investigate the biobehavioral consequences of disruption of the mother–infant relationships have focused primarily on the infant's responses. There have been relatively few reports that have examined the mother's response following separation. One of the first papers to emanate from this laboratory on this topic demonstrated that maternal cortisol was elevated following a brief 30-min separation although the mother remained in her familiar environment during the separation period (Mendoza *et al.*, 1978). There are other reports in the literature which also show a significant cortisol elevation in the mother as a consequence of removing the infant (Coe *et al.*, 1985). There are no reports that compared infant and maternal cortisol levels at identical time intervals following separation. Thus, we were concerned with comparing the time course of the infant and maternal cortisol response. In the present experiment, the response of the mother was of particular interest since one of the separation paradigms exposed the mother to persisent infant vocalizations.

GENERAL METHODS

Breeding Conditions

Adult female squirrel monkeys of Guyanese origin (*Saimiri sciureus*) were bred in our laboratory in large wire mesh cages (1.8 × 1.2 × 1.8 m). The monkeys were bred in groups of five to eight females, with one or two males. Once pregnancy was noted, the

males were removed and stable social groups of three to five pregnant females were formed. Each cage contained three sets of perches extending at varying heights for the length of the cage. Solid metal partitions divided adjacent cages. Cages were located in a temperature-controlled colony building with natural lighting. Wayne 25% Monkey Diet (Allied Mills, Inc., Chicago, IL) and water were available *ad libitum*. Vitamin supplements in a cherry-flavored liquid and fresh fruit were provided twice a week.

Behavioral Data Collection

All observations of behavior were recorded on check sheets from behind one-way vision glass. Depending on the nature of the behavior, data were recorded as the total frequency of occurrence (e.g., vocalization, eating, drinking) or by on-the-signal sampling at 30-sec intervals (e.g., activity). Data were analyzed by analysis of variance (ANOVA) procedures as described by Winer (1971) with the level of significance set at $p < .05$. Where appropriate, post hoc analysis for simple main effects and comparisons by Newman-Keuls procedures were performed.

Blood Collection and Hormone Assay

Blood samples were collected for plasma cortisol determination following rapid anesthetization with ether. A 0.5 ml sample was collected in a heparinized syringe with a small 25-gauge needle via cardiac puncture. This technique permits the rapid collection of samples within 2 min of cage disturbance and does not result in any long-term adverse effects. The blood was centrifuged for 20 min at 2000 rpm and the plasma frozen at −20°C until assayed. Cortisol was assayed by the radioimmunoassay method described by Klemm and Gupta (1975) using antiserum F3-314 from Endocrine Sciences (Tarzana, CA). Further details of blood sampling and radioimmunoassay procedures can be found in Coe *et al.* (1978).

EXPERIMENT 1

The following study assessed the behavioral and hormonal responses of mother and infant squirrel monkeys during the first 6 hr following separation.

Methods

Subjects. Five mother–infant dyads served as subjects. At approximately 5 wk postpartum, they were transferred to Wahman primate cages (61 × 61 × 91 cm) which contained two sets of perches. Each dyad was housed either with another mother–infant dyad or with a nonpregnant adult female. The dyads then remained undisturbed for the next 6 wk until testing was begun at 12 wk postpartum.

Procedure. When the infant reached 3 mo of age the behavioral and hormonal responses of mother and infant monkeys were assessed following separations of 1, 3, or 6 hr duration. Following an initial blood sample, collected at 1600h under nondisturbed conditions to determine basal cortisol levels, each dyad was subjected to the three separations (one per week). A mother and infant were removed from the home cage and placed in the adjacent observation cages (46 × 46 × 51 cm, with a single perch). Visual and tactile contact between mother and infant were prevented by a solid partition, but olfactory and auditory communication were permitted during the separation. Only a single dyad was tested on a particular day. All of the separations, whether 1, 3, or 6 hr in length,

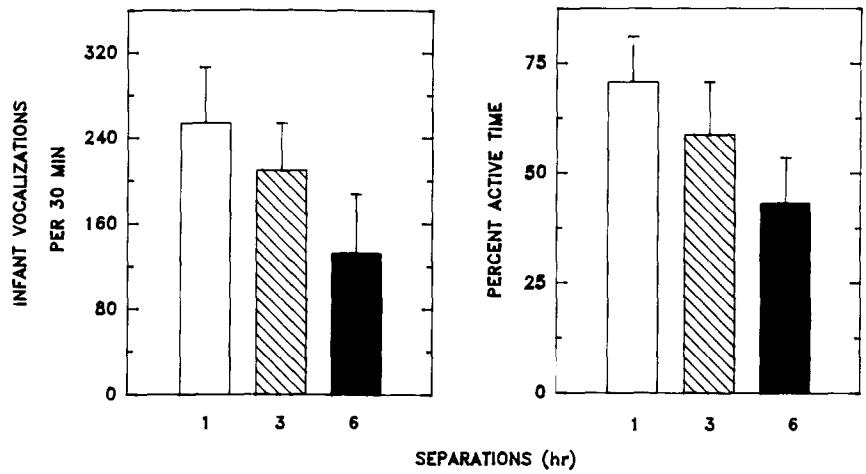

FIG. 1: Left: Frequency of infant vocalizations observed during last 30 min of separations from the mother lasting 1, 3, and 6 hr (Mean ± SEM, $n = 5$). Right: Percent of time the infant was observed active during the last 30 min of 1-, 3-, and 6-hr separations from their mother (Mean ± SEM, $n = 5$).

ended at 1600h to control for diurnal variations in cortisol levels at the time of blood sampling. Prior to blood sampling, behavioral observations for activity scores and frequency of species-specific infant isolation vocalizations were collected during the last 30 min of each separation (i.e., 0.5–1.0 hr, 2.5–3.0 hr, 5.5–6.0 hr). Following blood collection, the dyad was reunited and returned to the home cage. The order of the separation conditions was counterbalanced across subjects.

Results

Analysis of infant vocalizations indicated that infants emitted extremely high levels of the species-specific isolation peep, but that there was a significant decline in the rate of calling by 6 hr, $F(2, 8) = 4.94$, $p < .05$ (see Fig. 1). The infants also showed a decrease in agitated movement across time (72% of the time moving in the 0.5–1.0 hr period compared to 48% in the 5.5–6.0 hr period; see Fig. 1). However, the continuance of high activity in one infant at the later time point prevented this decline from reaching statistical significance. Similar to their infants, the mothers also showed a decrease in movement from the first to the sixth hour of separation (29% vs. 6% of the time spent moving), but again, individual variability precluded this change from attaining statistical significance.

In marked contrast to the decline with increasing lengths of separation observed in the behavioral response, the infants showed increasing plasma cortisol levels over time, $F(3, 12) = 27.05$, $p < .001$ (see Fig. 2). The mothers also increased their cortisol secretion after separation; but the values peaked at 1 hr and plateaued thereafter, $F(3, 12) = 16.84$, $p < .001$.

Discussion

The results of this experiment support the hypothesis that changes in squirrel monkey infant vocalization and the activity of the HPA axis may be inversely related under certain separation conditions. Thus, while the level of activity and vocalization decreased

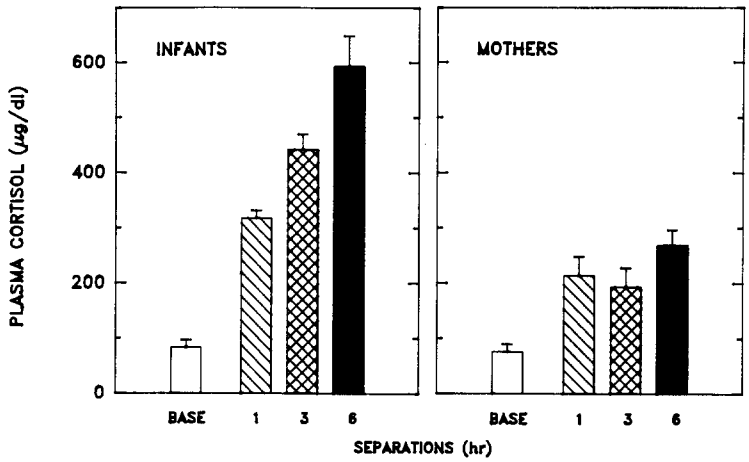

FIG. 2: Plasma cortisol levels of infants and mothers during undisturbed (BASE) conditions and following separations of 1, 3, and 6 hr (Mean ± SEM, $n = 5$).

over the 6 hr period, plasma levels of cortisol progressively increased in infants. These data may indicate a causal relationship (i.e., high levels of vocalizations serve as a coping response which reduces the activity of the HPA axis). However, there are other data which suggest that these two measures may be dissociated. For example, when squirrel monkey infants are repeatedly separated they show a marked decline in vocalizations across separations. This could be viewed as indicating habituation, but the plasma cortisol levels remain equivalently elevated even after six separations (Coe *et al.*, 1983a). It would appear that the behavioral response is much more malleable and susceptible to influence by environmental and experiential factors. Hennessy (1986) demonstrated that levels of cortisol remained unchanged in infant squirrel monkeys even after 80 brief separations. One condition that does result in a concomitant reduction in both the behavioral and hormonal responses, however, is to allow the separated infant to remain in its familiar environment with familiar social partners following removal of the mother (Coe *et al.*, 1985). It is possible that the responses elicited in these different separation paradigms reflect the operation of different processes. What is apparent is that vocalizations do not necessarily reflect the physiological state of the infant at least as measured by adrenocortical activation. These behaviors appear to have multiple functions. One such function may be to serve as a mechanism whereby the infant can reestablish contact and proximity to the mother. In monkeys, reunion with the mother leads to a relatively rapid return to baseline levels of adrenocortical and behavioral activity, while in rodents certain types of tactile contact can ameliorate the endocrine response to novelty (Levine & Stanton, 1990; Schanberg & Field, 1984).

Maternal cortisol levels were also significantly elevated. This increase was evident at 1 hr and persisted for at least 6 hr. However, the absolute levels in the mother were considerably lower than those observed in the infant and did not rise progressively over time. There are at least three possible explanations to account for the cortisol response of the mother. First, the mothers as well as the infants were placed in a novel environment and remained in this situation for the entire 6 hr. Exposure to novelty has been demonstrated to potently stimulate the HPA axis (Hennessy & Levine, 1979). Second, the

mother was exposed to the persistent vocalizations emitted by the infant. Third, in our early studies using the separation paradigm we showed that following a brief 30 min separation the mother's cortisol levels were elevated even though they remained in their home cage (Mendoza *et al.*, 1978) thus indicating that the loss of the infant may activate the maternal HPA axis.

EXPERIMENT 2

The purpose of this second experiment was to determine if the presence of the social partner (i.e., the infant) and its auditory cues influenced the mother's psychoendocrine responses. An additional aspect of this study was to extend the time interval following separation to compare the dynamics of the cortisol response to separation in both mothers and infants.

Methods

Subjects. Eight mother–infant dyads served as subjects. At approximately 6 wk postpartum the dyads were transferred to Wahmann cages, after which they were not disturbed further until testing began at 4 mo of age. Each dyad was housed with another dyad; however, only one mother–infant pair was tested at a time.

Procedure. Following an initial blood sample collected at 1600h under nondisturbed conditions to determine basal cortisol concentrations, each dyad was subjected to four separations (one per week). Dyads were separated for either 6 or 24 hr under two test conditions: total separation and adjacent separation. Total separation involved placing the mother and infant in individual observation cages located in different buildings in order to prevent any form of communication between the members of the dyad. A heat lamp was provided above the infant's cage during the night of the 24 hr separation. Adjacent separation replicated the procedure of Experiment 1, that is, mother and infant were placed in adjacent observation cages that permitted olfactory and auditory communication, but prevented visual and tactile contact. Food and water were available *ad lib* throughout testing. Behavioral observations, as described in Experiment 1, were collected during the last 30 min of the separation (i.e., 5.5–6.0 hr, 23.5–24.0 hr post-separation). A blood sample was taken from each member of the dyad immediately after the behavioral observations. Following sampling, the dyad was reunited and returned to its home cage. The order of presentation of the separation conditions was counterbalanced across subjects.

Results

As illustrated in Fig. 3, infants vocalized more frequently when they were placed in the cage adjacent to their mothers than when they were totally isolated from their mothers during separation, $F(1, 7) = 16.54$, $p < .01$. Most of the other behavioral measures (e.g., activity levels and occurrence of eating) were not significantly influenced by the type of separation. Separated infants, however, drank more when isolated than when adjacent to their mothers, $F(1, 7) = 12.40$, $p < .01$. The mothers displayed more signs of behavioral disturbance when their infants were proximal. Thus, for example, they showed higher levels of agitated movement after 6 hr of adjacent separation, as compared with that seen following the same period of total separation, $F(1, 7) = 5.80$, $p < .05$.

Analysis of plasma cortisol levels indicated that adrenocortical activity in infants and

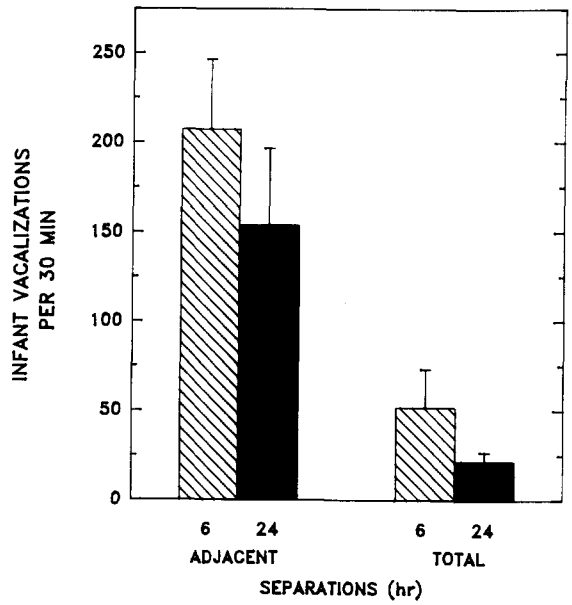

FIG. 3: Frequency of infant vocalizations observed during the last 30 min of 6- and 24-hr separations when the subjects were either adjacent or totally isolated (Mean ± SEM, $n = 8$).

mothers was significantly elevated over baseline following both types and lengths of separation, $F(4, 28) = 22.31$, $p < .001$ and $F(4, 28) = 8.59$, $p < .001$, respectively (see Fig. 4). The influence of the environment during separation was apparent in the extremely high corticoid levels (mean = 981 μg/100 ml) found in infants that underwent total isolation for 24 hr. In contrast, cortisol levels at 24 hr did not differ from those found at 6 hr, in separated infants that were housed adjacent to their mothers. The mothers did not show

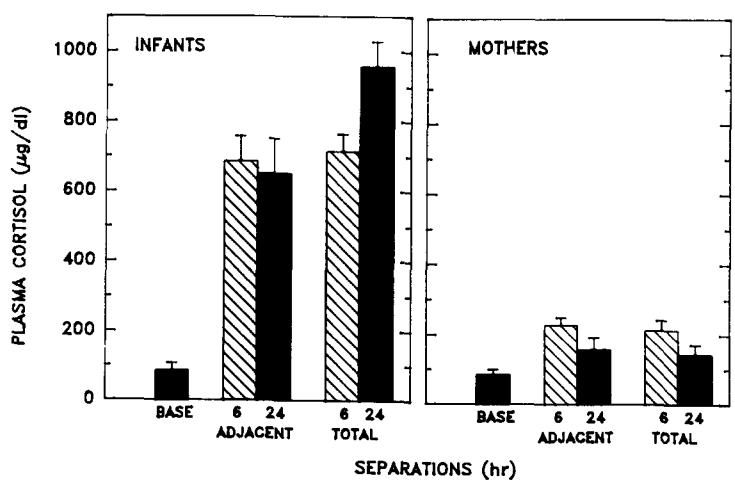

FIG. 4: Plasma cortisol levels (μg/dl) of infants and mothers during undisturbed (BASE) conditions and following separations of 6- and 24-hr under either adjacent or total separation conditions (Mean ± SEM, $n = 8$).

this differential corticoid response to the two separation environments. Moreover, unlike their infants, they showed a significant decrease in plasma cortisol at 24 hr as compared with levels observed at 6 hr, $F(1, 7) = 6.20$, $p < .05$.

GENERAL DISCUSSION

These results indicate that vocalizations and endocrine activity do not reflect identical aspects of the response to separation. Under certain conditions, the frequency of calling and the magnitude of the adrenocortical response appear to be inversely related, although not as strongly as observed in the first study. Thus, depending on whether one focuses on the 6 hr response or the 24 hr response, the interpretation of the relationship between calling and adrenal responses would have been considerably different. The data indicate that the behavioral and endocrine responses to separation may represent different processes that are only indirectly related. Rosenblum and Plimpton (1981) postulated that vocalization reflects the active attempts by the infant to reestablish contact and proximity with the mother. If the maternal cues are continuously present it might be expected that the infant would persist in engaging in these behaviors. In the absence of maternal cues, it might also be predicted that vocalizations would decrease more rapidly and eventually cease since they are not effective in obtaining the return of the mother. After 24 hr, vocalizations by the totally isolated infants were, in fact, minimal. Similar results have also been reported in rhesus macaques (Levine *et al.*, 1984, 1985).

The response of the HPA system appears to be more directly related to the level of disturbance evoked by the maternal loss, and thus is greatest when no maternal cues are available. We have postulated that for the infant, loss of the mother represents a loss of psychological control, which has been demonstrated to be a potent activator of the HPA system (Levine & Ursin, 1991). The young infant's initial experience with contingencies and with processes designed to modulate and reduce arousal fall within the context of the mother–infant relationship. Even at an older age, the primary response the infant uses to lower its arousal levels during disturbing and stressful situations is to maintain contact or proximity with the mother. Such contact, for example, has been shown to dramatically reduce HPA activity within 1 hr following a brief period of separation (Coe *et al.*, 1985). During an involuntary separation, reunion with the mother is no longer possible and thus its primary coping response cannot be utilized. This is reflected by persistent elevations of plasma cortisol levels.

The mothers, in contrast to their infants, appeared to be considerably less responsive and exhibited a different pattern of HPA activity following separation from their infants. In Experiment 1 the levels of cortisol peaked at 1 hr but remained at these levels 6 hr later. In the second study the mothers appeared to be returning to basal levels by 24 hr. Furthermore, there was no evidence that being exposed to an infant that was constantly vocalizing had any effect on the mother's cortisol response. Thus, maternal cortisol levels were identical regardless of whether they remained adjacent to, or totally separated from, their infants. These findings suggest that the mothers in this study were reacting primarily to the disturbance of handling and novelty. However, evidence from previous studies does suggest that the loss of the infant can be a pertinent stimulus which activates the maternal HPA system. Mendoza *et al.* (1978), for example, reported elevations in cortisol in mothers who remained in their home cage following removal of the infants. Cortisol was acutely elevated following removal of the infant when the mothers were permitted to remain in their social group (Coe *et al.*, 1985). Within the context of the

present studies we can not determine whether the cortisol response of the mother occurred as a consequence of exposure to novelty, loss of the infant, or an interaction of these two factors.

The differences between mothers and infants in the magnitude of circulating cortisol may be explained in a number of ways. They may, for example, reflect a diminished capacity of the infant to clear stress-induced levels of cortisol from the circulation. This is certainly one possibility, since one of the physiological mechanisms responsible for the exceptionally high levels of cortisol found in the squirrel monkey is altered hormone metabolism and a slow clearance rate (Klosterman *et al.*, 1986). However, clearance and metabolism probably cannot completely account for the inordinately high cortisol values, since separated infants continued to show increases in cortisol levels at 24 hr (Fig. 4). Furthermore, they can sustain these elevated levels for at least 2 weeks (Wiener *et al.*, 1992). Alternatively, the observed differences might reflect changes in the negative feedback action of cortisol on the brain and the pituitary. Under normal (adult) conditions, high levels of cortisol suppress the release of corticotropin releasing factor (CRF) and arginine vasopressin (AVP) from the hypothalamus, and adrenocorticotropic hormone (ACTH) from the pituitary, eventually leading to a drop in circulating cortisol. While this does occur in the mother, it does not appear to occur in the infant for at least 24 hr following maternal separation. This may be due to immaturity of the feedback system in the infant. In this respect, the older infant monkey may be similar to the weanling rodent for which there is evidence that the negative feedback system is not as efficient as in the adult (Goldman *et al.*, 1973). Finally, it can be postulated that the stress of maternal loss is so intense and persistent that the HPA system remains continually activated.

In our laboratory we have never observed cortisol values in an adult squirrel monkey that approximate those seen in infants. Administration of pharmacological doses of ACTH results in cortisol levels that are well below those observed in infants following separation. We believe that maternal loss is indeed a profoundly disturbing event for the infant and would therefore maximally activate the HPA system. However, we also believe that the infant's exaggerated adrenocortical response to separation reveals that there are important components of the HPA axis, related to hormone clearance and negative feedback, that are probably immature.

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