Effects of Maternal Mobility, Partner, and Endocrine State on Social Responsiveness of Adolescent Rhesus Monkeys

CLARK O. ANDERSON
Department of Psychology
University of California
Santa Barbara, California

ANN McM. KENNEY
Department of Psychology
University of Florida
Gainesville, Florida

WILLIAM A. MASON
Psychology Department
and
University of California Primate Research Center
Davis, California

The social behavior of rhesus monkeys raised for the 1st year of life with mobile (MS) or stationary (SS) cloth surrogate mothers was investigated when the animals reached 4-5 yr of age. The MS males generally refrained from social interaction during initial pairings with females, whereas SS males interacted frequently, but were more often the targets of attacks and chases from adult females than were MS males. The MS males were more likely to vary their social behavior according to the behavior of the social partner and seemed to benefit more from extended social exposure than their SS counterparts. The MS females were more similar to wild-born females than were SS females in nearly every behavior category and dimension tested. These results suggest that rearing with mobile artificial mothers improves the chances of later adaptive social adjustments in socially restricted monkeys.

Early restriction of social contacts can produce a broad spectrum of deficiencies and aberrations in the social behavior of rhesus monkeys (e.g., Alexander & Harlow, 1965; Anderson & Mason, 1974; Harlow & Harlow, 1962; Mason, 1960, 1961a, 1961b; Miller, Caul, & Mirsky, 1967; Missakian, 1969; Mitchell, 1968). As yet, however, the nature and importance of the specific factors that are involved in the development of

Reprint requests should be sent to Dr. William A. Mason, Psychology Department, University of California, Davis, California 95616, U.S.A.

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species-characteristic norms of social competence are poorly understood (e.g., Chappell & Meier, 1974; Meier, 1965).

Many approaches to this problem are possible, no one of which is sufficient to identify more than a few significant rearing variables or establish their specific role in the ontogeny of social behavior. The approach taken in this research was to simulate a limited maternal attribute, namely nonspecific "passive movement stimulation," and to examine the developmental consequences of this rearing variable over a relatively long time span and in a variety of situations. Results for the first 14 months indicated that compared to monkeys raised with stationary surrogates those raised with mobile artificial mothers showed less stereotyped body-rocking, played more on their surrogates, were bolder in approaching humans, and were somewhat more likely to approach and interact with wild-born monkeys (Mason & Berkson, 1975). Moreover, at a later age (28 months), monkeys raised with mobile surrogates spent more time looking at other macaques than did monkeys raised with stationary surrogates and were more sensitive to the visual attributes of stimulus animals (Eastman & Mason, 1975).

The aim of the present research was to assess the social behavior of some of these same surrogate-raised monkeys at the age of 4-5 years by comparing them with each other and with a like-age group of wild-born animals. With male subjects, the effects of extended experience with the partner and its age, gender, and endocrine state were examined (Experiments I and II); with female subjects, the effects of partner's age and subject's endocrine state were investigated (Experiment III).

Experiment I

Method

Subjects. Nine male rhesus monkeys (*Macaca mulatta*) were equally divided into 3 groups: a wild-born (WB) group, housed singly from their arrival in the laboratory at an estimated age of 8-12 months and 2 lab-born groups, separated from their mothers within the first 2 days post-partum and raised in individual cages with identical cloth surrogates. The surrogates of one group (SS) occupied a fixed position within the cage, whereas those for the other (MS) moved up and down and around the cage on an irregular schedule (see Mason & Berkson, 1975, for further details).

At about 311 days of age the surrogates were permanently removed. The monkeys were maintained in individual cages, except for testing. Prior to this experiment, social interactions for lab-born monkeys were limited to a series of paired encounters beginning when they were approximately 14 months old and totaling 5.5 hr of social exposure, equally divided between male and female wild-born companions (Mason & Berkson, 1975). Some of these same wild-born monkeys were used in the present research. Their living arrangements and experiences in the laboratory were comparable to those of the lab-born groups. In addition, just before the present tests, males from the 3 groups were each paired for a total of 3 hr with 3 ovariectomized adult females, 2 of which served as social stimuli in the present experiment.

Lab-born males were about 40 months old when testing began (MS: mean = 37.4, range = 36-40 months; SS: mean = 42.4, range = 3847 months). Ages for the wild-born males were estimated to fall within the range of the lab-born males.

Social Stimuli. Five wild-born monkeys served as test animals. Four of these were ovariectomized females: 2 juveniles (each had begun menstrual bleeding at least 2 months prior to the beginning of testing) and 2 adults. The 5th social stimulus was an intact juvenile male.

Apparatus. Pair encounters occurred in a large outdoor tunnel cage (14 x 2 x 2 m). Equal sections (1 x 2 m) marked on the cage floor were used to locate individual monkeys and to derive a measure of inter-animal distance. Transport cages were fitted to 2 guillotine doors at one end of the tunnel cage. Observations were from behind a 1-way screen centered 4.6 m from the front of the tunnel cage. Timers and counters were located behind this screen.

Procedure. Tests were conducted in 2 phases. In the 1st phase, 2 females (1 juvenile, 1 adult) were treated subcutaneously (s.c.) with 20 μg/.2 ml peanut oil/day of estradiol benzoate (EB) and the other 2 were given s.c. only .2 ml peanut oil/day. Treatments were reversed during the 2nd phase. Twelve days intervened between the beginning of the new treatment conditions and the start of the 2nd phase.

On each of the 5 test days within a phase every male was paired for 5 min with each of the 5 stimulus monkeys before the next subject was tested. During a 5-min test locations were noted at the beginning of each 15-sec interval and specific social responses of both monkeys were recorded once during each 15-sec interval in which they occurred. Duration of mounts with thrusting was measured to the nearest .1 sec. Response categories and their descriptions (see Table 1) are essentially the same as those used in many other investigations of rhesus social behavior (Hinde & Rowell, 1962; Mason, 1960).

Order of testing was partially balanced across rearing groups and order in which the stimulus animals were presented was balanced across subjects and rearing groups. The subjects were admitted into the test cage before the stimulus monkeys.

Data Analysis. Frequency of 15-sec intervals in which a response occurred was divided by the maximum possible number of intervals (= % occurrence). Mean duration of mounts with thrusting was obtained by dividing total duration by the number of discrete intervals in which this response occurred. All data were subjected to standard analyses of variance in a repeated-measures design, with subjects repeated across stimulus conditions. Scores were transformed when necessary to normalize distributions ($X' = \sqrt{X} + \sqrt{X+1}$ for frequencies; $X' = \log_{10} [X + 1]$ for durations). In the event a statistically significant group effect was obtained, intergroup comparisons were made by the Newman-Keuls test; tests of simple main effects (Winer, 1971) were carried out following significant interaction terms.

Results

Effects of Rearing Conditions on Behavior with Females. Abnormal stereotyped behaviors, such as rocking, self-clasping, and self-biting, were not shown by WB males and were shown significantly less frequently by MS than by SS males. These data (Fig. 1A) agree with findings on the same animals at an earlier age (Mason & Berkson, 1975).

With respect to social behavior with female partners, the sharpest contrasts occurred between the WB males and the 2 lab-born groups (Table 2). Proxemic responses were most frequent for WB pairings as were specific affiliative behaviors. The WB males

TABLE 1. Behavior Categories.

Abnormal stereotyped self-directed responses
Chews, bites, sucks, or clasps own body or body-rocks while in a seated or crouched posture.
Proxemic responses
Approach: Comes to within arms' reach of partner. Contact: Any part of one animal's body touches that of partner. Proximity: Pair members are stationary and within arms' reach of each other, but not touching. Withdraw: Moves directly away from partner after being in contact or proximity.
Affiliative responses
Brace: Maintains a rigid stance on all fours and supports mounting partner. Groom: Systematically picks through partner's hair. Mount: *Attempted* (places hands on partner's side or back preparatory to mount); *complete* (has hands on partner's hips or sides and foot-clasps both of partner's legs); and *incomplete* (is either oriented inappropriately, or fails to clasp both of partner's legs). Play: Approach-withdrawal (rapidly approaches partner and withdraws) and wrestles, pulls or bites the partner, unaccompanied by threats, screams, or barks. Presentation: Buttocks and tail elevated and directed toward partner.
Agonistic responses
Attack/chase: Hits, bites, pushes, grabs or pursues partner while making threats; actor runs toward a withdrawing companion while threatening. Grimace/scream: Retraction of lips resulting in a "grin-like" expression, or high "ee" sound often accompanied by a grimace. Threat face: Mouth open, teeth usually covered; often accompanied by a direct stare, head-bobbing or head thrusts toward partner, and a loud, explosive vocalization (bark).

scored higher for approach (Fig. 1B), contact (Fig. 1C), attempted mounts (Fig. 1D), and completed mounts (which occurred only in the WB group). Intergroup differences on these measures were statistically significant. The WB males also made significantly more attacks/chases on females (Fig. 1E) and elicited more presentations and grimace/screams from them than did either lab-born group.

The data suggest that the amount and intensity of social interaction were somewhat higher in the SS group than in the MS group (Table 2). Every SS male scored higher than any MS male on measures of approach (Fig. 1B), proximity (Fig. 1D), contact (Fig. 1C), groom, and attempted mounts (Fig. 1D). Only SS males initiated social play (2/3), or attacks/chases (2/3); these males also elicited more attacks/chases from females and responded more frequently with grimaces/screams. In fact, the only measure in which the score of every MS male was higher than that of any SS male was threats received from females. Although quantitative differences were for the most part slight, they were consistent with the observers' impression that the SS males were more "impulsive" or "precipitate" than the MS males; the latter seemed to be more cautious in their approach to social interaction and more responsive to the behavior of their companions.

Effects of Hormone Treatment of Females. Although EB treatment had no reliable effects on proxemic responses, it influenced social contacts in the direction of

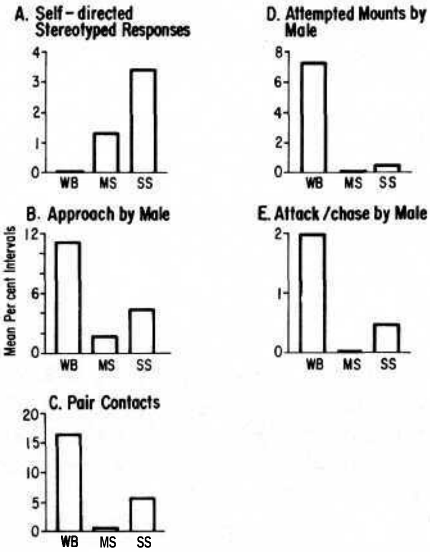

Fig. 1. Experiment I: Mean percentage of 15-sec intervals in which the indicated responses occurred (pairings with females).

TABLE 2. Responses (Mean % Intervals) from Pairings of Wild-Born (WB), Mobile Surrogate (MS) and Stationary Surrogate (SS) Males with Juvenile (J) and Adult (A) Wild-Born Females (Experiment I).

	WB			MS			SS		
	J	A	Mean %	J	A	Mean %	J	A	Mean %
Response									
Proximity	2.7	1.5	2.1	1.9	.1	1.0	5.2	.4	2.8
Contact	21.9	10.5	16.2	.8	.3	.5	12.6	.8	6.7
Males									
Approach	10.2	12.6	11.4	3.1	.4	1.7	7.7	.4	4.1
Groom	1.3	.9	1.1	.0	.0	.0	2.2	.1	1.1
Play	1.4	.0	.7	.0	.0	.0	3.7	.0	1.8
Attempt mount	7.1	8.0	7.5	.0	.0	.0	1.0	.0	.5
Complete mount	5.7	7.5	6.6	.0	.0	.0	.0	.0	.0
Threat	3.8	.5	2.1	2.8	2.8	2.8	.1	2.6	1.3
Grimace/scream	1.2	.0	.6	.5	.5	.5	.3	2.2	1.3
Attack/chase	3.8	.2	2.0	.0	.0	.0	.8	.1	.5
Females									
Approach	4.3	.6	2.5	2.7	.8	1.7	6.3	.8	3.6
Withdraw	6.2	1.8	4.0	3.0	.3	1.7	9.2	.1	4.7
Present	2.1	10.2	6.1	1.7	.4	1.0	2.3	1.2	1.8
Brace	4.7	7.4	6.0	.0	.0	.0	.0	.0	.0
Threat	2.7	1.2	2.0	5.4	4.4	4.9	.8	4.0	2.4
Grimace/scream	8.8	.5	4.7	.1	.3	.2	.1	.4	.2
Attack/chase	.3	.1	.2	.8	.4	.6	.8	.8	.8

sex-related activities. The WB males showed an increase in grooming (.2% vs 2.2%), as did SS males (.1% vs 2.2%). The MS males showed no grooming, which resulted in a significant Treatment x Group interaction ($p < .05$). Attempted mounts by WB males (5.1% vs 10.0%) and SS males (.3% vs .7%) were also more frequent when females were EB treated (Treatment x Group interaction, $p < .05$). The average duration of mounts with thrusting by WB males and the frequency with which adult females braced for WB males also increased (Treatment x Group interaction, $p < .005$). Play frequencies during EB decreased in the WB group (1.4% vs 0%) and the SS group (3.3% vs .3%).

During EB, frequencies of grimace/scream by males and females and attacks/chases by males declined, although these effects were not significant. The frequency of attacks/chases initiated by females, however, was significantly related to the males' rearing history and to the females' age and endocrine state. The EB increased frequencies of attacks/chases by adult females toward SS but not toward MS or WB males (see Fig. 2). In contrast, juvenile females during EB treatment showed lower frequencies of attacks/chases toward WB and SS males and higher frequencies toward MS males (Treatment x Age x Group interaction, $p < .025$).

Effects of Age Class of Female Partner. Proxemic responses were higher in pairings with juvenile females than with adult females (see Table 2; significant for female approach and withdrawal, contact, and proximity), social distance was significantly lower, and grooming and play by WB and SS males were more frequent. Self-directed behaviors by MS and SS males were also significantly less frequent with juvenile females than with adult females.

Effects of Sex of Juvenile Social Partners. The level of social activity in all groups was generally higher with the juvenile male than with juvenile females (significant for approaches, attacks/chases by both subject and stimulus monkey; see Table 3). The largest effect of partner's gender, however, was on the MS males. For example, more than 93% of total contacts in the MS group were with the juvenile male as compared to 52% for the other 2 groups (Group x Stimulus interaction, $p < .01$). Similarly, all of the MS group's grooming responses were directed toward the juvenile male, whereas the other 2 groups directed all grooming toward juvenile females (Group x Stimulus

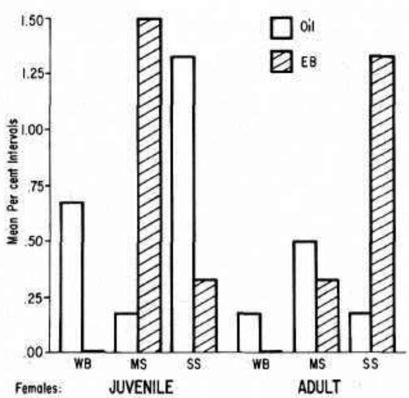

Fig. 2. Experiment I: Mean percentage of 15-sec intervals in which the female attacked or chased males from the 3 rearing groups during treatment with oil or EB.

TABLE 3. Responses (Mean % Intervals) from Pairings of Wild-Bom (WB), Mobile Surrogate (MS) and Stationary Surrogate (SS) Males with Male (M) and Female (F) Wild-Born Juveniles (Experiment I).

	WB		MS		SS	
	M	F	M	F	M	F
Response						
Contact	24.0	21.9	10.3	.7	13.7	12.6
Subjects						
Approach	21.5	10.2	4.0	3.1	11.7	7.8
Groom	.0	1.3	2.7	.0	.0	2.2
Play	6.3	1.4	.0	.0	.8	3.7
Attempt mount	10.2	7.1	1.7	.0	2.7	1.0
Complete mount	7.2	5.7	.7	.0	.0	.0
Threat	2.7	3.8	.8	2.8	.3	.1
Attack/chase	13.7	3.8	.7	.0	1.3	.8
Stimulus Monkeys						
Approach	.7	4.3	8.3	2.7	10.5	6.3
Present	1.5	2.1	.5	1.7	3.2	2.3
Threat	7.2	2.8	.5	5.4	.7	.8
Attack/chase	3.5	.3	6.0	.8	4.7	.8

interaction, $p < .05$); all mounting attempts by the MS group (attributable entirely to 1 male) were with the juvenile male, as compared to 73% and 59%, respectively, for the SS and WB groups. Furthermore, of the 10 mounting attempts by the MS males, 4 resulted in complete mounts. In contrast, no complete mounts were observed in the SS group. The male stimulus also provoked attacks/chases from 2 of the MS males, whereas no MS monkey showed such behaviors with females. The juvenile male also made significantly more approaches to lab-born monkeys than did juvenile females (Group x Stimulus interaction, $p < .025$).

Experiment II

Although the results of Experiment I indicated that the MS males' level of social interaction was the lowest of the 3 groups, the relatively large differences in the behaviors of these males toward the juvenile females and the juvenile male suggested that they were also more sensitive to differences in the behavior of their companions than the SS monkeys. In fact, the more cautious "wait and see" approach of the MS males to the social situation suggested they were the more adaptable of the 2 lab-born groups and had at least as good potential for achieving species-characteristic social behavior as the SS males. To test this possibility we gave all groups supplementary exposure to the 2 juvenile females of Experiment I and then retested them. We expected MS males to profit most from this experience.

Method

During supplementary exposure females were not treated. Males were paired twice with each female in an outdoor cage (3.6 x 3.6 x 1.8 m), 2-3 hr at each pairing, for a total of 10 hr of exposure per male equally divided between the 2 females. Subsequently, males were paired with the same females in 2 test series of 3 days each in the apparatus used in Experiment I. During the first series, 1 female received daily EB injections (20 μg/.2 ml peanut oil/day) and the other received the oil vehicle only (.2 ml/day); treatments were reversed for the 2nd series. Each pair was tested once a day for 10 min. Test order for males and presentation order of females were partially balanced within a test series; order of testing was the same in both series. Recording procedures were as in Experiment I. Because total observation times were different in Experiments I and II, the data were adjusted to permit statistical comparison.

Results

Proxemic responses generally increased in Experiment II as compared to Experiment I. Females approached males significantly more often (4.4% vs 9.8%) and, as anticipated, the corresponding changes in male behavior were most dramatic in the MS group. The MS males made significantly more approaches in Experiment II than in Experiment I and, in fact, surpassed the other 2 groups on this measure (see Fig. 3). Contacts also increased significantly for MS males between Experiments I and II although the level was below that of the WB or SS males (see Fig. 3).

Similar changes were noted in specific social responses. Male grooming increased significantly (1.7% vs 6.9%, combined groups) and 2 of the MS males groomed females in Experiment II although none had done so in Experiment I. Corresponding with the significant increase in play by females, all MS males played in Experiment II whereas none had done so with these females in Experiment I. Their average score (4.4%) was higher than that of the WB group (2.1%) although below that of the SS group (5.9%). Mounting attempts were made by all MS males in Experiment II whereas none had attempted to mount these females in Experiment I. The percentage of attempted mounts was the same in the 2 lab-born groups (.3%) which was well below that of the

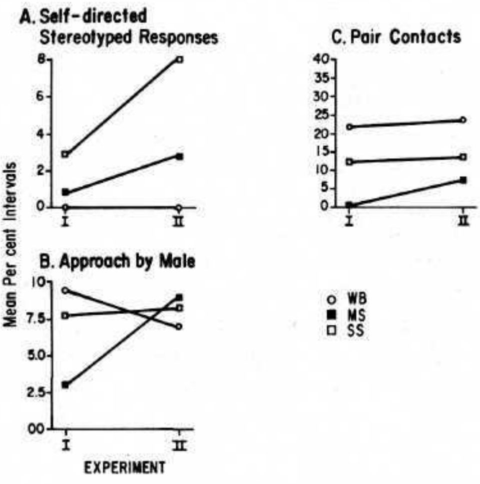

Fig. 3. Experiments I and II: Mean percentage of 15-sec intervals in which the indicated responses occurred in pairings of juvenile females with males from the 3 rearing groups.

WB group (1.8%). In contrast to Experiment I, however, in which 1 MS male made 4 complete mounts with the juvenile male, no monkey in the lab-born groups achieved a complete mount. Two MS males attacked or chased females in Experiment II–none had done so in Experiment I–and the level of agonistic responses (1.0%) was between that of the WB (2.3%) and SS (.4%) groups.

The frequency of self-directed stereotyped behaviors in the lab-born groups was not reduced by increased familiarity. On the contrary, these behaviors were about 3 times more frequent in Experiment II than in Experiment I (see Fig. 3).

Female endocrine treatment did not affect the frequency of complete and attempted mounts. The mean duration of mounts with thrusting by WB males, however, increased from 5.4 sec to 19.3 sec (Treatment x Group interaction, $p < .05$). Whereas in Experiment I the frequency of attacks/chases by juvenile females during EB increased toward MS males and decreased toward WB and SS males, in this experiment attacks/chases toward all groups were lower during treatment (1.8% vs .7%).

Experiment III

Method

Subjects. Twelve bilaterally-ovariectomized female rhesus monkeys were tested in Experiment III–4 each from the WB, MS, and SS groups. All females had the same social experience as the comparable groups of males; 2 WB females had additional experiences serving as the juvenile social stimuli in Experiments I and II.

Laboratory-born females were about 51 months of age at the start of testing (MS: mean = 53.9, range = 48-63 months; SS: mean = 47.1, range = 41-60 months); WB females were matched in age as closely as possible to the lab-born groups. Menstrual bleeding had been detected in all females prior to ovariectomy about 4 months before the start of testing. One female from the MS group was tested nearly 2 months later than the other females owing to a precautionary quarantine imposed on her following possible exposure to infected monkeys.

Social Stimuli. Four wild-born males served as test monkeys. Three of these animals were from the wild-born group tested in Experiments I and II. Two males were classified as "late" juveniles and 2 as "early" juveniles, based on differences in canine development.

Procedure. Tests were conducted in 2 series in the apparatus described for Experiment I. In each series, starting at least 5 days before and continuing throughout the 4-day test sequence, 2 females from each rearing group were treated daily with EB (20 μg/.1 ml peanut oil/day s.c.), whereas the other 2 received oil vehicle only (.1 ml/day s.c.). Treatments were reversed during the 2nd series.

Females were tested in fixed trios (except for 1 test group which lacked the quarantined MS female), each trio containing 1 female from each rearing group. Each female was paired every day in 4 successive 5-min periods with each of the stimulus males. Test order among trios and presentation order for males were completely balanced within each series. The male was admitted into the test cage first.

Behavior categories were identical to those in Experiments I and II. In addition, behavioral characteristics were rated on 3 of the 4 test days of each series, for a total of 6 ratings for each pair. Four characteristics were rated, each on a 4-point scale (0 to 3): male and female interest in the partner (0 = inattentive to partner to 3 = very attentive to partner); initiation of social interaction by the female (0 = social activities not initiated to 3 = social activities frequently initiated); fear of the male partner (0 = no sign of fear to 3 = strong avoidance or submission); severity of male aggression (0 = no attacks or chases to 3 = intense attack or chase episodes).

Data Analysis. The frequency data were analyzed by standard variance procedures using a repeated-measures design with subjects repeated across the 4 stimulus conditions. Frequency scores for each female with each class of stimulus male in each treatment condition were normalized when necessary and averaged. Ratings were averaged for each experimental condition (rearing group of female, age class of male, treatment) and analyzed by the Mann-Whitney test (Siegel, 1956).

Results

Rearing Conditions. Proxemic responses were generally less frequent in pairings with lab-born females than with WB females and differences between groups were significant for frequency of male and female approaches, male withdrawals, proximity, and contact (see Table 4).

A similar trend was evident for specific affiliative behaviors. Males made reliably more mounting attempts and complete mounts with WB females than with lab-born

TABLE 4. Responses (Mean % Intervals) from Pairings of Wild-Born (WB), Mobile Surrogate (MS) and Stationary Surrogate (SS) Females with Early Juvenile (E) and Late Juvenile (L) Wild-Bom Males (Experiment HI).

	WB			MS			SS		
	E	L	Mean %	E	L	Mean %	E	L	Mean %
Response									
Proximity	9.6	5.7	7.7	5.3	2.3	3.8	2.8	.1	1.4
Contact	33.8	18.6	26.2	9.9	4.7	7.3	3.8	2.6	3.2
Females									
Approach	8.9	7.4	8.2	4.6	1.3	3.0	3.9	.3	2.1
Withdraw	16.8	8.1	12.5	8.5	5.1	6.8	11.0	4.6	7.8
Present	7.1	7.5	7.3	5.9	2.5	4.2	1.9	1.3	1.6
Groom	11.3	8.7	10.0	.7	.4	.5	.0	.0	.0
Play	7.0	.2	3.6	5.0	.0	2.5	.3	.0	.2
Threat	.1	.3	.2	.7	1.5	1.1	.1	.1	.1
Grimace/scream	.5	5.2	2.8	12.9	20.8	16.8	16.9	21.6	19.3
Attack/chase	.2	.0	.1	.2	.7	.5	.1	.1	.1
Males									
Approach	24.4	14.8	19.6	16.5	9.4	12.9	9.6	4.9	7.3
Withdraw	16.6	14.1	15.4	12.3	5.4	8.8	2.6	.9	1.8
Attempt mount	17.6	10.5	14.0	4.2	1.6	2.9	.8	.2	.5
Complete mount	12.7	8.8	10.8	.3	.0	.2	.1	.0	<.1
Threat	.4	<.1	.2	.4	.6	.5	.1	.1	.1
Grimace/scream	.1	.1	.1	.1	.0	<.1	.0	.0	.0
Attack/chase	6.2	2.1	4.1	6.4	6.0	6.2	10.6	7.5	9.1

females (see Table 4). Complete mounting of lab-born females was hampered by the tendency of these monkeys to crouch or withdraw in response to male mounting attempts. In contrast, WB females tended to brace in response to mounting.

The frequency of agonistic behaviors also differentiated WB and lab-born females. Males attacked or chased lab-born females more often than WB females; lab-born females also grimaced and screamed more frequently than WB females (see Table 4). In keeping with these findings, ratings indicated that lab-born females were significantly more fearful than WB females.

Early experience with a mobile surrogate mitigated many of the effects of early social deprivation. Abnormal stereotyped behaviors were significantly less frequent in the MS than in the SS group (.5% vs 6.9%). Furthermore, proxemic responses were higher in pairings with MS than with SS females. Scores for proximity and contact were significantly higher for MS than for SS females: males approached and withdrew from MS females significantly more often; MS females were rated significantly higher than SS females in initiating social interaction; of the lab-born monkeys, only MS females groomed (see Table 4). With respect to sexual responsiveness in the lab-born groups, MS females presented more frequently; only these females braced when males attempted to mount; and they were mounted more frequently.

The lab-born groups also differed in agonistic behaviors. The MS females attacked and chased males more frequently, were less often targets of male attacks and chases, and grimaced or screamed less frequently than SS females. These findings are supported by the ratings which indicated MS females were significantly less fearful than SS females.

Age Classification of Male. Proxemic responses were generally more frequent in pairings with early juvenile males than with late juvenile males (see Table 4). Frequencies of approaches and withdrawals by both males and females and of proximity and contacts were significantly higher with early than with late juvenile males. Ratings of female attentiveness to partner were also significantly higher with early juveniles.

Specific affiliative behaviors—play, attempted and complete mounts by the male—were significantly more frequent in pairings with early than with late juvenile males (see Table 4). Although early juvenile males attacked and chased more frequently than did late juvenile males, ratings of intensity of male aggression and female fearfulness were lower than in pairings with late juveniles.

Estradiol Treatment. During EB treatment, contacts and ratings of female initiation of social interaction increased and social distance decreased, as compared to the control conditions. All changes were statistically significant. All specific affiliative behaviors, except play, also increased during EB treatment. Increases in sex presentations by females and attempted mounts by males were statistically significant.

As shown in Figure 4, females were more likely to brace to attempted mounts during EB treatment. This effect was influenced by the female's rearing history and by the age class of the male (Treatment x Age x Group interaction, $p < .05$ based on transformed data: $X' = \arcsin \sqrt{\text{percentage}}$). The SS females never braced in response to mounting attempts and MS females braced mainly during EB treatment and only in response to mounting attempts by young juvenile males. In contrast, WB females braced for both classes of males, regardless of treatment conditions. The EB increased the frequency of bracing by WB females to mounting attempts, significantly so to late juvenile males.

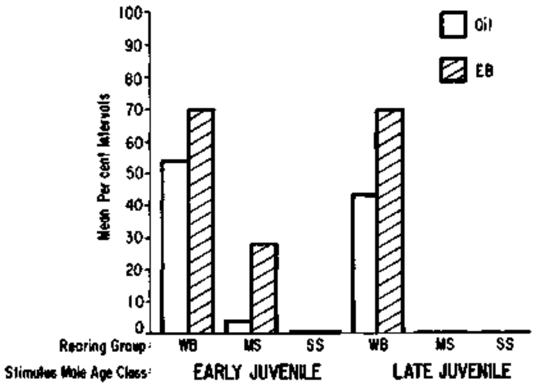

Fig. 4. Experiment III: Mean percentage of male mounting attempts to which females from the 3 rearing groups braced during treatment with oil or EB.

The frequency of many agonistic behaviors declined during EB. Ratings of fear and frequencies of abnormal stereotyped behaviors by MS and SS females also declined significantly.

Discussion

These results demonstrate that the presence of a mobile artificial mother during the 1st year of life has abiding effects on the social development of rhesus monkeys. Although the MS and SS monkeys were both socially aberrant as compared to their WB controls, the 2 lab-born groups differed in many respects most of which indicated some mitigation of the effects of early social deprivation in the moving surrogate group.

The ameliorative influence of surrogate mobility was most evident in females. Social behavior of MS females was closer quantitatively and qualitatively to that of WB females in virtually every respect. Most of these differences can probably be ascribed to greater emotional arousal in SS females, particularly in response to social contact. The SS females received significantly higher ratings for fearfulness, made fewer approaches, and were involved in fewer social contacts. Although females in all groups appeared bolder and more tolerant of social contacts during EB treatment, no SS female braced in response to male mounting attempts, regardless of her endocrine state, whereas MS females did so with the younger males, mainly during treatment with EB. These findings clearly suggest that surrogate mobility increased the likelihood of biologically effective mating in females. They also illustrate how seemingly modest variations in rearing conditions can have important and unanticipated long-range effects on the relations between behavior and endocrine state.

The effects of surrogate mobility on male responsiveness were not as clear and are more difficult to characterize simply. In Experiment I, SS males were more active in close-range social transactions with females than were MS males, but they also elicited more attacks/chases by females than either the MS or WB groups. These data are consistent with our impression at the time that SS males were "impulsive" or "under-controlled," tending to initiate and accept approaches regardless of the disposition of the female. As a result, SS males used flight to terminate most social interactions, often dashing the length of the test cage, or leaping into the air (frequently accompanied by self-biting). In contrast, MS males seemed more attentive to the characteristics of the social partner–in keeping with the data on looking behavior (Eastman & Mason, 1975). Compared to their behavior with females, MS males were much more forthcoming in their pairings with the juvenile male, no doubt a reflection of the large differences between his behavior and that of the females. With female partners–which generally appeared to be rather tense in Experiment I–MS males maintained a discreet distance and made only a few tentative social responses. Changes in the females' endocrine state had no significant effects on the behavior of these males–probably owing to their strategy of maintaining distance from females–whereas EB treatment resulted in more frequent grooming and mounting attempts by SS and WB males and longer durations of mounting with thrusting by WB males. In view of the serious deficiencies in sexual performance of most socially restricted males, less importance should probably be attached to the failure of MS males to respond differentially to female endocrine states than to the fact that 4 mounting attempts by an MS male (all with the juvenile male) involved proper orientation with double foot-clasping. This integration of several motor components of mounting suggests that surrogate mobility had beneficial effects on sexual performance of some males, as well as females.

A further suggestion that different strategies describe the approach of MS and SS males to social situations is provided by the changes in their behavior with the same juvenile females between Experiments I and II. Following extended exposure to the females, MS males showed substantial increases in approaches, contacts, grooming, mounting attempts, aggressive interactions, and play. These changes in the behavior of MS males corresponded to changes in approach and play by the females. In contrast, the social behavior of the SS males showed relatively little change between experiments, a finding similar to Missakian's (1972) results. Whether further experience would continue to affect the social behavior of MS and SS males differentially is an interesting question. We believe that it would.

Notes

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