

Early experience affects the intergenerational transmission of infant abuse in rhesus monkeys

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Maternal abuse of offspring in macaque monkeys shares some similarities with child maltreatment in humans, including its transmission across generations. This study used a longitudinal design and a cross-fostering experiment to investigate whether abusive parenting in rhesus macaques is transmitted from mothers to daughters and whether transmission occurs through genetic or experiential factors. Nine of 16 females who were abused by their mothers in their first month of life, regardless of whether they were reared by their biological mothers or by foster mothers, exhibited abusive parenting with their firstborn offspring, whereas none of the females reared by nonabusive mothers did. These results suggest that the intergenerational transmission of infant abuse in rhesus monkeys is the result of early experience and not genetic inheritance. The extent to which the effects of early experience on the intergenerational transmission of abusive parenting are mediated by social learning or experience-induced physiological alterations remains to be established.

child maltreatment | animal models | cross-fostering | development | primates

One of the most striking characteristics of child maltreatment is its transmission across generations. An estimated 20–30% of abused children are likely to become abusive parents themselves, whereas estimates of abusive parents who have an early history of abuse can be as high as 70% (1–4). The mechanisms through which child abuse is transmitted across generations are unclear. The social learning view is that abused children acquire the maltreatment behavior patterns through observational learning, modeling, and reinforcement (3). According to attachment theorists, what it is transmitted across generations is not behavior but a cognitive model of the parent–child relationship, which in turn affects behavior (5). Early child abuse can also result in long-term alterations in neuroendocrine development and emotion processing (6–8), and such alterations may increase the probability of displaying abusive parenting in adulthood. Finally, genotype also may play an important role in the intergenerational transmission of child abuse (9).

Research on the intergenerational transmission of child abuse and its underlying mechanisms is hampered by the presence of many confounding variables and the difficulty of conducting experiments. Some of these difficulties can be overcome with the use of an animal model. Child maltreatment is not unique to humans but has been observed in some species of nonhuman primates as well (10). Infant abuse by socially deprived rhesus macaque (*Macaca mulatta*) mothers was first documented in the laboratory by Harlow and his collaborators (11). More recent research has shown that in large populations of rhesus and pigtail macaques (*Macaca nemestrina*) living in captive social groups, 5–10% of all infants born every year are physically abused by their mothers (12, 13). Infant abuse occurs in the first few months of infant life and manifests itself as infant dragging, crushing, throwing, stepping, sitting on, or biting (14). The consequences of abuse range from superficial scratches and bruises to serious injury and death. Abusive mothers alternate short bouts of abuse with long periods of appropriate caregiving behavior and do not

show any gross abnormalities in their social interactions with their conspecifics. Mothers who have abused their offspring in the past are likely to repeat the same patterns of behavior with their successive infants, suggesting that abusive parenting is a relatively stable maternal characteristic (15). Most patterns of infant abuse are qualitatively distinct from any other behaviors in the maternal repertoire and are never exhibited by most individuals within a population, including first-time mothers who sometimes exhibit clumsy behavior with their infants (e.g., they hold them upside down). Therefore, abusive mothers and their behavior are readily identifiable. Infant abuse also has been observed in free-ranging rhesus macaques (unpublished observation) in both captive and free-ranging Japanese macaques, *Macaca fuscata* (16–18), and in primates other than macaques (19). Therefore, infant abuse is not a by-product of a particular captive environment or specific to macaque monkeys.

Infant abuse in monkeys shares several similarities with child abuse in humans, including its prevalence in the population, the relation between age and vulnerability to abuse, some psychological characteristics of abusive mothers, and the role of psychosocial stress in triggering abuse (10). In rhesus and pigtail macaques, infant abuse is concentrated in some matriline and among closely related individuals such as mothers and daughters or sisters (12–13). The distribution of infant abuse within the population is consistent with the hypothesis that it is transmitted across generations along the maternal line, e.g., from mother to daughter. This intergenerational transmission of abuse in group-living monkeys, however, has never been documented with a prospective longitudinal study.

The goal of this study was to investigate whether rhesus macaque females who abuse their offspring produce daughters who are likely to become abusive mothers themselves. To investigate the relative contribution of genetic inheritance and early experience, some females were cross-fostered at birth between abusive and nonabusive mothers, whereas others were reared by their biological mothers (a similar approach is described in ref. 20). All females were observed during infancy, and their exposure to abusive parenting was documented. When these females gave birth to their first live offspring, the quality of their own maternal behavior and, in particular, the occurrence of infant abuse, was analyzed in relation to their early experience and their birth condition.

Materials and Methods

Subject Recruitment. This study was conducted with female rhesus macaques from a population of >1,500 individuals living at the Field Station of the Yerkes National Primate Research Center in Lawrenceville, GA. The Yerkes Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care. The subjects lived in several different social groups and were housed in 38 × 38 m outdoor compounds with indoor housing areas. The groups consisted of 30–35 adult females with their immature offspring and 2–5 unrelated adult males. All

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Table 1. Age, parity, and dominance rank of the mothers in the four experimental groups

Group	Age, years	No. of previous offspring	Dominance rank, high rank/total
Control/control	9.44 ± 3.97	4.44 ± 2.69	5/9
Abuse/control	7.43 ± 1.51	3.14 ± 1.34	3/7
Control/abuse	11.44 ± 3.91	5.78 ± 2.58	6/9
Abuse/abuse	9.12 ± 2.80	5.00 ± 2.07	5/8
Test	$F(3,29) = 1.98$, NS	$F(3,29) = 1.82$, NS	$\chi^2(3) = 0.79$, NS

NS, not significant.

groups had a stable matrilineal structure and a linear dominance hierarchy. Female dominance ranks were assessed by using data on unidirectional aggression and submission that were collected during previous studies.

Sixteen of 21 female infants were successfully cross-fostered between abusive and nonabusive mothers within 24–48 h after birth (see ref. 21 for details of the cross-fostering procedure). Seven female infants born to multiparous mothers with a history of abusive parenting were adopted and reared by unrelated control mothers (abuse/control group), whereas nine female infants born to control mothers were adopted and reared by abusive mothers (control/abuse group). Five more abusive mothers failed to adopt infants, whereas all of the control mothers successfully adopted infants. The number of subjects in the abuse/control group, however, was limited by the availability of female infants born to abusive mothers during the study period. Cross-fostered infants were reared in groups different from those in which their biological mothers resided.

The abusive mothers who served as study subjects had been observed in previous years and their abusive behavior had been documented (14, 15). Only mothers whose frequency and severity of abuse did not jeopardize their infant's life were used for this study. These abusive mothers were typically consistent in the frequency and severity with which they abused offspring born in successive years (15). Control mothers were selected opportunistically among multiparous females from other social groups who gave birth to a female infant within 24–48 h of the abusive mothers and had no previous record of abusive parenting. In one case, a primiparous mother was used for lack of alternatives. In this case, we made sure that no instance of infant abuse had previously been reported in the subject's matriline or observed in the time interval between the subject's parturition and the cross-fostering procedure.

Eight rhesus macaque females who were born to abusive mothers and reared by them (abuse/abuse group) and nine females who were born to control mothers and reared by them (control/control group) also were used as subjects. The 8 abused subjects were selected from a database of 47 abused infants who were observed during their first few months of life during the course of other studies conducted during 1994–2002. All of these studies were conducted by the same research team and with similar procedures of observation. Eight abused females were selected from the database as subjects for this study because they survived into adulthood, and gave birth to surviving offspring, and information on the quality of their maternal behavior (abusive vs. nonabusive) was available. The other 39 individuals from the database were excluded because they were male ($n = 22$) or they were female but died before reproducing ($n = 7$), had not yet given birth ($n = 6$), or had given birth but no reliable information on the quality of their maternal behavior was available ($n = 4$). Similar to the abusive mothers in the control/abuse group, the abusive mothers in the abuse/abuse group typically exhibited rates of abuse that did not jeopardize their infants' survival. Nine control females were selected from a similar database of 44 nonabused infants because they survived

into adulthood, and gave birth to surviving offspring, and information on the quality of their maternal behavior (abusive vs. nonabusive) was available. The other 35 individuals from the database were excluded because they were male ($n = 20$), or they were female but died before reproducing ($n = 2$), had not yet given birth ($n = 12$), or had given birth, but no reliable information on the quality of their maternal behavior was available ($n = 1$). The age, parity, and dominance rank of the mothers in the abuse/control, control/control, abuse/abuse, and control/control groups were not significantly different (Table 1).

Observation Procedures. For all of the infants in the four experimental groups, with one exception, behavioral data were gathered with the focal sampling and the behavior sampling methods (22) during weekly or monthly observation sessions. The observers were tested for reliability before the beginning of data collection. Using the focal sampling method, the observers recorded the behavior of the focal infant and that of its mother on a continuous basis. The behavior sampling method was used to record every occurrence of infant abuse within the social groups in which the subjects lived. The exception was one subject in the control/abuse group, for which no focal observations were made. Information collected with the behavior sampling method, however, established that this subject was abused by its foster mother. Analysis of behavioral data collected with the focal sampling method focused on hourly rates of maternal abuse as well as hourly rates of the following maternal behaviors: making contact, breaking contact, cradling, grooming, restraining, and rejecting. Infant abuse was operationally defined as dragging (the mother drags her infant by its tail or leg while walking or running); crushing (the mother pushes her infant on the ground with both hands); throwing (the mother throws her infant a short distance with one hand while standing or walking); hitting (the mother violently slaps her infant with one hand or arm); biting (common definition); stepping or sitting on (the mother steps on her infant with one foot or both feet, or sits on her infant) (see ref. 14 for discussion and definitions of other maternal behaviors).

Information gathered with the behavior sampling method was used only to assess whether an infant was abused by its mother. When the subjects gave birth to their first live offspring, they were observed with the same procedures for 3–4 months. The observers were not blind to the early life treatments of the cross-fostered infants but had no clear expectations about to the outcome of study. One control/abuse subject died at the age of 1.5 years because of injuries sustained in a major outburst of aggression within her group and was therefore excluded from the study. One abuse/control subject also was excluded from the study because she had two miscarriages in two consecutive years and has not yet given birth to a surviving infant. For one subject in the control/abuse group and one subject in the abuse/abuse group, no focal data on maternal behavior could be collected. However, information gathered with the behavior sampling

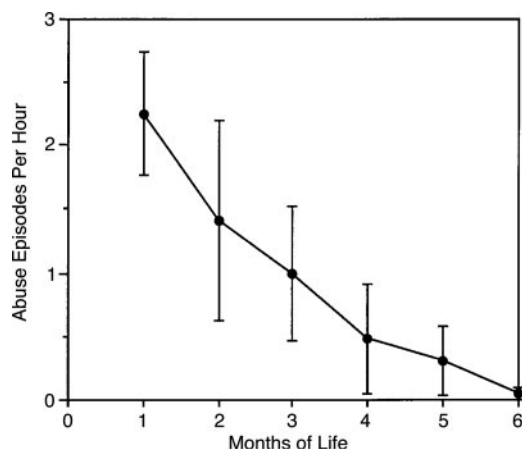


Fig. 1. Hourly rate of abuse (mean per individual \pm SE) experienced by abused females, both cross-fostered and non-cross-fostered, in their first 6 months of life.

method established that both subjects abused their firstborn offspring.

Results

All of the subjects reared by abusive mothers, including the cross-fostered infants, were abused by them, whereas none of the others were. The rate of abuse (number of episodes per hour) was not significantly different between cross-fostered abused infants and infants who were reared and abused by their biological mothers (cross-fostered, mean = 2.43, SD = 1.77; non-cross-fostered, mean = 1.85, SD = 2.27; Mann-Whitney U test, $N_1 = 7$, $N_2 = 8$, $U = 17$, $P > 0.20$).

Fig. 1 shows the time course of infant abuse in the first 6 months of life in all abused subjects (Friedman's ANOVA, $\chi^2 = 30.28$, df = 5, $P = 0.0001$). Abuse was most frequent in the first month and decreased steadily with age (Spearman's correlation, $r = -1.0$, $n = 6$, $P = 0.02$). In five cases, abuse ceased by the end of month 1; in no case was abuse observed after the end of month 6. Abused infants were not treated differently than controls by their peers.

Fig. 2 shows the prevalence of abusive parenting when the females gave birth to their first live offspring (age, mean = 4.00 years, SD = 0.44, range 3–5 years). Nine of the 16 females who were reared by abusive mothers exhibited abusive parenting with their own offspring, whereas none of the 15 females reared by the

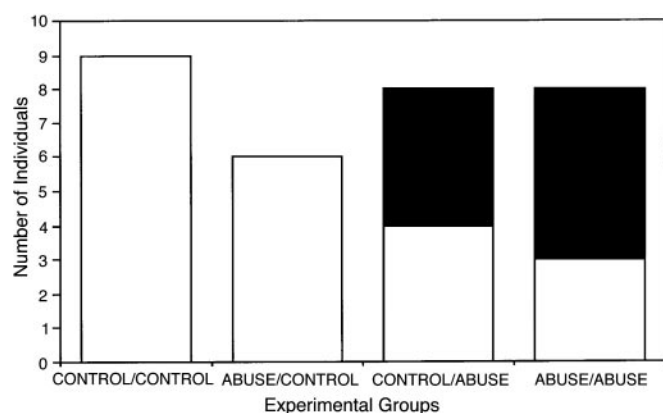


Fig. 2. Number of individuals who exhibited abusive parenting (black) and who did not exhibit abusive parenting (white) with their first offspring in the four experimental groups.

control mothers did (Fisher's exact probability test, $P = 0.0006$). In particular, the subjects in the control/abuse group, who had the abuse experience without the abusive mothers' genotype, were more likely to become abusive mothers than the females without the abuse experience, regardless of their genotype ($P = 0.007$). For one subject in the abuse/abuse group, abusive parenting resulted in infant death in the first week of life.

There was no significant difference in the hourly rate of infant abuse in the first month of life, when most of the abuse occurred, between the abused females who became abusive mothers ($n = 8$, mean = 2.57, SD = 2.52) and the abused females who did not exhibit abusive parenting in adulthood ($n = 7$, mean = 1.60, SD = 1.17; $U = 26$, $P > 0.50$). Furthermore, there were no significant differences in any other aspects of maternal behavior during the same period between these two groups of individuals. Finally, there was no significant difference in the number of infant siblings females had before giving birth for the first time (abusers, mean = 2.44, SD = 1.13; nonabusers, mean = 2.14, SD = 1.34; $N_1 = 9$, $N_2 = 7$, $U = 25$, $P > 0.50$), suggesting similar opportunities for learning through observation of their siblings.

Discussion

The results of this study demonstrate that rhesus macaque mothers who abuse their offspring produce daughters who are likely to become abusive mothers themselves. Specifically, 9 of the 16 females reared by abusive mothers exhibited abusive behavior with their firstborn offspring, whereas none of the females reared by control mothers did. Although the behavior of first-time mothers may be different from that of older and more experienced females, second-generation abusive parenting was clearly not the result of maternal inexperience or clumsiness associated with primiparity, because the females reared by abusive mothers and those reared by controls were equally young and inexperienced when they first gave birth. In addition, previous studies have shown that macaque mothers who abuse their firstborn offspring continue to exhibit similar patterns of abuse with all of their successive offspring (12, 13, 15), thus suggesting that maternal inexperience is not a primary cause of abuse.

The occurrence of abusive parenting among females who were cross-fostered at birth between abusive and nonabusive mothers suggests that the intergenerational transmission of infant abuse from mother to daughter is likely to be mediated by early experience and not by genetic inheritance. Abused females may learn the patterns of abusive behavior through direct experience with their mothers and later repeat these patterns with their own offspring. Abused females also may learn patterns of abusive behavior through observation of their mothers with their younger siblings. Another possibility is that early infant abuse results in long-term alterations of neural circuits or neuroendocrine processes that directly or indirectly affect the expression of maternal behavior (23).

Not all of the females who were reared and abused by abusive mothers exhibited abusive parenting with their firstborn offspring. This finding is in line with human research on child maltreatment, which shows that only 20–30% of abused children are likely to become abusive parents themselves (1–4).

In this study, the females who became abusive mothers received higher rates of abuse in infancy than those who did not become abusive mothers, although the difference was not statistically significant. In humans, it is not known why some abused human children become abusive parents, whereas others do not, although recent evidence suggests that genetic factors may affect the extent to which victims of child abuse develop antisocial behavior or personality disorders later in life (9). Our lack of understanding of individual differences in vulnerability to early abuse does not necessarily imply that early adverse experience is not an important factor in the transmission of child abuse across

generations. Instead, it suggests that early adverse experience may predispose individuals to display later abusive parenting but that whether abused individuals are particularly vulnerable or resilient may depend on the presence of other risk or protective factors, which may be biological or environmental, or both. Further research with a primate model of child maltreatment can address the specific mechanisms by which early experience affects the intergenerational transmission of infant abuse as well as the role of other risk and protective factors in determining individual differences in vulnerability or resilience.

In addition to highlighting the role of early experience in the intergenerational transmission of infant abuse, this study also demonstrates that cross-fostering studies can be a powerful tool for investigating the role of genotype and environment in the development of primate behavior. Cross-fostering studies are more difficult to perform in nonhuman primates than in rodents (20). Nevertheless, this study shows that under particular experimental conditions, monkey mothers can be successfully induced to adopt and rear unrelated infants. Macaque mothers probably learn the characteristics of their own offspring shortly after parturition, and successful adoption may depend more on elevated maternal motivation than on failure to discriminate unrelated infants from their own offspring (24). Once infants are

successfully adopted, however, they are reared by their mothers as if they were their biological offspring. For example, the rate of infant abuse in this study was not significantly different in cross-fostered and non-cross-fostered infants. Moreover, abusive mothers abused their adopted infants with rates similar to those exhibited with their own biological offspring in previous years (21).

Because experimental cross-fostering studies cannot be easily conducted with humans, nonhuman primates provide unique animal models for the study and understanding of the development of human behavior. The availability of a primate model of child maltreatment provides the opportunity not only to conduct research on the causes and consequences of this phenomenon but also to test various forms of intervention and therefore contribute to its prevention.

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