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Comparison of Adopted vs. Biological Mother-Infant

Relationships in Nonhuman Primates

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A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

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Department of Psychology

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ABSTRACT

Comparison of Adopted vs. Biological Mother-Infant

Relationships in Nonhuman Primates

Rachel A. Bogh

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Studies suggest that adoptees are at risk for a number of psychopathological behaviors. To understand the etiology of this risk, 150 socially housed rhesus macaques were studied, including 107 infants reared with their biological mothers and 43 infants reared with unrelated adoptive mothers. Mother-infant behaviors were recorded across the first 6 months of life. Analyses were performed using a hierarchical linear mixed model. All reported results were tested at $p<0.05$. Adopted infants were observed on average to approach and leave their mothers more frequently, explore the environment and locomote longer, exhibit more anxiety-like behavior, spend less time being held to their mother's breast, and were rejected by their mothers more when compared to nonadopted infants, indicating they are more likely responsible for maintaining the relationship. They also direct and receive more noncontact aggression on average to other social group members, and showed evidence of higher anxiety exhibiting high levels of anxiety-like self-directed behavior when compared to nonadopted infants. Also, results indicate that adopted infants have significantly lower levels of the CSF serotonin metabolites 5-hydroxyindoleacetic acid when compared to nonadopted infants.

Keywords: adoption, rhesus macaques, primates, mother-infant relationship, serotonin, 5-HIAA, CSF, temperament, attachment, psychopathology

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CONTENTS

Comparison of Adoptive vs. Biological Mother-Infant Relationships in Nonhuman Primates

Studies report adopted children as having more psychiatric problems as compared to nonadopted children (Moore & Fombonne, 1999; Wegar, 1995), which may reflect on the adoptive mother-infant relationship. Also, in an adoption overview in 2005, parents report adopted children engage in more “acting out” behaviors and are more likely to perceive adopted children as having temperamental problems when compared to nonadopted children (Nickman et al., 2005). These studies suggest that adopted children may have conflicting temperaments with their adoptive parents, and as such, are more likely to engage or be perceived as engaging in “acting out” behaviors (Nickman et al., 2005). Consequently, adoptive mother-infant relationships may require more effort for the pair to achieve what Chess and Thomas (1991) called a goodness of fit.

The mother-infant relationship has been a major focus in psychology (Bowlby, 1969; Suomi, 2005). While a large literature exists for the study of mother-infant/parent-infant interactions in infants reared by their biological parents as well as infants reared without mothers, studies of the effects of adoption are limited. In a study involving adoption in rhesus macaques, rejection and contact breaking behaviors by adoptive mothers to their infants were higher when compared to nonadoptive mothers (Champoux, Boyce, & Suomi, 1995), suggesting an environmental component, but little more research has been performed. More recently the focus has moved from the gene vs. environment of maternal treatment to gene-environment interactions and the subsequent development of the child (Bennett et al., 2002; Champoux et al., 1995; Barr et al., 2008). A large number of studies have demonstrated that child development does not exclusively occur through either nature or nurture, but rather the child’s phenotype is more typically an interaction between the two (Barr et al., 2003).

One could posit that adopted infants' temperament and, possibly as a consequence, attachment to their mother are affected by adoption. The purpose of this study is to assess behavioral and genetic effects on mother-infant relationships by comparing rhesus macaque infants reared by a nonrelated adoptive mother to rhesus macaque infants reared by a biological mother.

Nonhuman Primates and Adoption

The use of nonhuman primates to study the mother-infant relationship has been in practice for several decades (Harlow & Zimmerman, 1958). Human and nonhuman primate research concerning behavior, genetics, brain structure, and biochemistry are analogous and even homologous (shared ancestry (Bennett et al., 2002)), and primate behavioral data is similar enough to human behavior to be published in the same journals and conferences (Higley, 2003).

Infant nonhuman primate development is similar to though quicker than human development (e.g. monkeys at 6 months of age correlate roughly to humans at 2 or 3 years of age). Thus the study of nonhuman primate development gives a comparative perspective to human development (Maestripieri, 2003). For example, both human and nonhuman primates live in large social groups, cooperate to use natural resources, have a primary caregiver (generally mother) who long-term cares for infants, and show individual characteristics representative of temperament (Maestripieri, 2003).

Adoption studies in nonhuman primates can be used to model many aspects of human mother-infant behavior outcomes (Maestripieri, Megna, & Jovanovic, 2000). The infant may be fostered to another lactating mother for practical or experimental reasons (i.e., the infant is without a mother, or specifically to model human adoption in non-human primates

(Bartolomucci et al., 2004)). Nonhuman primate research can be beneficial in modeling human adoption with the added ability to control environmental variables, and lead to a better understanding of the long-term emotional, behavioral and physiological outcomes of adoption on both the mother and infant in the relationship.

Behavioral Observations of the Mother-Infant Relationship

As established in the literature, important behavioral aspects of the mother-infant relationship include temperament (Goldsmith et al., 1987) and attachment (Ainsworth, Blehar, Waters & Wall, 1978; Bowlby, 1969), which can be reviewed through a model first described by Chess and Thomas (1991). The goodness of fit model proposed by Chess and Thomas (1991) is used to explain successful and difficult interactions between parent and child, specifically in terms of the parent's and child's temperaments. If a relationship is successful, parent and child interactions mesh well together to achieve the success in the relationship and the relationship is seen as having a goodness of fit. Goodness of fit may be useful in describing relationship quality (i.e. attachment) between an infant and caregiver (generally the mother in nonhuman primates), and will be used hereafter to describe the quality of the mother-infant relationship, by means of temperament and attachment.

Temperament. The temperament, or the characteristic patterns of emotional reactivity unique to an individual (Thomas & Chess, 1977), of the mother and infant play a significant role in their relationship quality. While it is widely held that the development of temperament is biologically based, it is clear that over time interactions with the caregiver modify its expression and the acquisition of the more mature personality (Ainsworth & Bowlby, 1989). Since the development of the infant is at least in part a result of their experiences with the caregiver, negative or positive reactions by the caregiver to the infant's behavior largely influences the infant's eventual personality. The infant's temperament can fit in a glovelike fashion with the caregiver's personality or it can be conflictual, ultimately determining the "goodness of fit" of the parent-infant relationship (Chess & Thomas, 1991). Some infants' temperaments, according to Chess and Thomas, are difficult regardless of the personality and capabilities of the parents and lead to a more arduous relationship. Particularly for infants with difficult temperaments, the goodness of fit depends on the sensitivity and behavior of the parent as well as the infant's temperamental ability to adapt (Chess & Thomas, 1991)

Attachment. Ultimately, the goodness of fit in the mother-infant relationship may affect the quality of the bond between the mother and infant and the paramount attachment quality. Attachment specifically refers to the strong affectionate or emotional tie between the primary caregiver and infant (Bowlby, 1969).

The attachment bond that occurs in the mother-infant relationship is influenced by the dynamic interplay of the infant's temperament and parental treatment of the infant (Hinde & Spencer-Booth, 1967). In order to study mother-infant attachment, Ainsworth (1978) set up an experiment called the "strange situation" and from the findings categorized 4 different attachment styles: (1) secure attachment; (2) avoidant; (3) resistant; and (4) disorganized/disoriented attachment. Secure attachment is most frequently seen in both human and nonhuman primates (Hinde, 1975), and is formed by the infant to its caregiver when the caregiver acts sensitively to satisfy the infant's unique needs and adapts according to the developmental stage and temperament of the infant (Hinde & Spencer-Booth, 1967; Ainsworth & Bowlby, 1989). It is also described by Ainsworth (1978) as infants who prefer parents to strangers, seek contact with parent after brief separation, and reliably use the parent as a secure base.

Whether adoptive or nonadoptive mothers, attachment quality between the mother and infant is important to the goodness of fit in the mother-infant relationship. Discordant attachment bonds can lead to maternal rejection of infant, mother-infant relational discord, aggression, as well as infant learned helplessness and antisocial behaviors (Maestripieri, 2003). All of these behaviors decrease the infant's chances of survival.

Contact Comfort and the Secure Base. In order to investigate the basic needs of nonhuman primate infants, Harlow and Zimmerman removed infant monkeys from their biological mother and reared them on wire and cloth mother surrogates (Harlow & Zimmerman, 1958). In what was surprising at the time, the infants preferred the nonfeeding cloth mother to the wire mother in almost every setting. Even though food was only available from the wire mother, almost immediately after feeding the infants would return to the cloth mother surrogate (Harlow & Zimmerman, 1958). From this observation, Harlow came to believe that the mother's physical touch, her warmth—also referred to as contact comfort—is important and perhaps requisite for the infant's development. Consistent with Bowlby's (1953) claims that infants need mother warmth and intimacy, Harlow believed that contact comfort leads to a secure attachment because it reduces arousal.

Also, an infant may feel secure in their mother's presence and explore the environment, and leave her immediate presence believing they have their mother as a "secure base" to reliably return to at all times. Harlow demonstrated in his surrogate studies that contact comfort is the keystone of the secure base that the mother provides. The goodness of fit of the mother-infant relationship is influenced by the infant's ability to find security in their mother's presence. Through arousal reducing mechanisms that the mother provides—such as vestibular stimulation, warmth, and physical contact—she can become a secure base for the infant to return home to through consistent acceptance of her infant; consequentially, as the infant becomes secure with their mother, they will explore novel settings if their mother is present. As the infant matures, mothers that sensitively respond to their infant's need produce infants that become increasingly self-reliant in regulating their own arousal, resulting in independence through the encouragement of their mother as a secure base (Harlow & Zimmerman, 1958; Hinde & Spencer-Booth, 1967). Ultimately, infants become securely attached to their caregiver as their caregiver adjusts their behavior to fill the infant's needs. As an infant receives contact comfort, the mother becomes a secure base for the infant, which establishes the goodness of fit in the mother-infant relationship.

Adoption

The relationship between good mothering and the mother-infant goodness of fit raise questions of the efficacy of adoption. When Thomas and Chess spoke of the goodness of fit model, they spoke in conjunction with the temperament of the individuals involved in a relationship (Thomas & Chess, 1977). All mothers, adoptive and nonadoptive, must deal sensitively with their infants' temperament and behavior. Thomas and Chess would predict that without shared genes (e.g. adoption), mothers must exert more effort to be sensitive to the infant's temperament (which is more likely to be dissimilar to their own) and adjust their behavior more often to fit the infant's needs in order to achieve a harmonious, goodness of fit in the mother-infant relationship (Thomas & Chess, 1977).

Gene-Environment Interaction

Temperament and attachment generally define the infant's developmental environment, and since the mother-infant relationship is also biological, interest has formed in the gene-environment (GxE) interaction. For instance, in primates, mother-infant separation (defined by the mother temporarily leaving her infant (Shannon et al., 2005)), can cause a stressful experience that alters the infant's phenotype, and as a consequence changes the temperament and normal behavior of the infant. This is observed in infant monkeys' high crying rates and self-directed behavior, when compared with infants receiving normal treatment (Fairbanks, 1989). Also, early in life influences can have long-term effects which may occur in adopted and nonadopted mother-infant relationships (Maestripieri, Lindell, & Higley, 2007).

Serotonin Transporter Gene. GxE interaction studies are increasingly interested in the serotonin transporter gene (Champoux et al., 2002). The serotonin transport gene codes for the amount of serotonin transporters in an organism, which in turn modulates the amount of serotonin neurotransmitters available, as measured by concentrations of 5-hydroxyindoleacetic acid in the cerebrospinal fluid (Heils et al., 1996). There are two basic allele length variations (that this study will discuss) on the serotonin transporter gene linked polymorphic region (5-HTTLPR), the long and short. The short variation leads to less transcription of the serotonin transporter, meaning it can modulate less extracellular serotonin than the long allelic variation (Heils et al., 1996).

In a study measuring serotonin neurotransmitter metabolites, Maestripieri and colleagues found that a mother's treatment can have an effect on many aspects of her offspring's phenotype, including altered phenotypic expression (Maestripieri et al., 2007). Early treatment may also alter neurotransmission. In their second year of life, adopted macaque daughters were measured for concentrations of the serotonin metabolite 5-hydroxyindoleacetic acid, and analysis showed higher rates of maternal rejection by the adoptive macaque mother resulted in low serotonin metabolite levels in the adopted daughters when compared to other adoptees who were rejected less. This is significant because regardless of the presence or absence of deleterious serotonin modulating genotypes (i.e. short serotonin allele), high rates of rejection from their mothers led to lower CNS serotonin activity (in comparison to monkeys who were rejected less). Hence, regardless of the type of allele inherited for serotonin transporter coding, long-term serotonin functioning can be phenotypically influenced by maternal treatment (Maestripieri et al., 2007; Bennett et al., 2002; Barr et al., 2003; Higley et al., 1993).

Hypotheses

This study compares adoptive vs. nonadopted mother infants relationships, in light of temperament, attachment, genotype, and cerebrospinal fluid (CSF) serotonin content. I expected that (1) on average adopted infants would more likely have different temperaments from their adoptive mother, and as a result be more responsible for maintaining the relationship with their adoptive mother than infants reared with their biological mother who share on average 50% of their genes. (2) Also as a result of different temperaments between adopted infants and their adoptive mothers, adopted infants would receive more rejections from their mother, and as a consequence spend less time in close proximity to their mother, give and receive aggression more often in relating to other monkeys as compared to nonadopted infants. (3) Since adopted infants are more likely to be rejected by their adoptive mother, adopted infants would exhibit more anxiety—as measured by self-directed behavior, freezing, vocalizations, and stereotypies—than will nonadopted infants. And (4) since the phenotypic expression of the serotonin transporter genotype is environmentally-dependent and particularly susceptible to stress, adopted infants' serotonin activity would lower in comparison to nonadopted infants, and will be a product of GxE interaction with high rates of rejection interacting with genotype.

Method

Subjects

The subjects are 145 socially housed rhesus macaques, 102 of which were reared in social groups with their biological mother and 43 fostered to an unrelated adoptive rhesus mother. The subjects were part of an ongoing longitudinal study designed to investigate biobehavioral outcomes. These studies were conducted by two laboratories located in Poolesville, MD, the Laboratory of Comparative Psychopathology and the Laboratory of Comparative Ethology in the National Institutes of Alcohol Abuse and Alcoholism and Child Heath and Human Development.

All mothers were multiparous. Adoptive mothers had given birth within a week of the fostering procedure. This fostering procedure is the technique used for adoption in many nonhuman primate laboratories, particularly those with macaques (Champoux et al., 1995). To facilitate the adoption, the infant was removed from its mother and positioned in a monkey transport cage placed outside the potential adoptive mother's cage. The mother had to enter the transport cage to fetch the infant. If she retrieved the infant, the dyad was then monitored for closely 24 hours for signs of rejection or inappropriate maternal behavior. If the infant did not nurse during this period, it was removed and returned to its biological mother or placed in a neonatal nursery facility. The fostering procedure occurred within three days of the infant's birth in order to prevent the mother from rejecting the infant. Adopted infants were randomly assigned to unrelated adoptive mothers based on their date of birth and the adoptive mother's date of giving birth.

Rearing

Infant rhesus macaques (n=145) were reared in indoor-outdoor enclosures with their mothers in mixed-sex social groups containing two adult males and six to eight adult females with their infant offspring. The indoor-outdoor enclosures measured 2.44x3.05x2.21 m (indoor) and 2.44x3.0x2.44 m (outdoor) and the floors of both were covered in wood chips with lights in the indoor portion maintained on a 12:12 cycle (7:00 a.m. to 7:00 p.m.). The animals in the social groups were fed high-protein monkey chow and received water ad libitum. Supplemental fruit was provided three times each week; sunflower seeds were presented daily (Shannon, 2005). The sample included infants from thirteen birth-year cohorts (e.g. cohorts represent the different years the infants were born) born at the facility between 1991 and 2005. Infants were always fostered to a female outside of their own birth group.

Behavior Scoring

Mother-infant behaviors were recorded across the first six months of life. Focal behavioral scoring was performed in 5-minute sessions. Infants were scored two times a week in the social group for the first 24 weeks of life. All behaviors were scored in duration (seconds) with the exception of mother-infant approaches and withdrawals, rejections, vocalizations, and aggression, which were scored in frequency. The 5-minute sessions were averaged across month, giving one measurement per month for six months. Behavioral observations were made by multiple observers, who achieved interobserver reliabilities of 85% or greater. On rare occasions, it was necessary to remove an animal from the group for medical observations or as a result of equipment failure, in which data for the animal was not obtained.

The behavioral categories were designed to measure mother-infant relations, anxiety, psychopathology, overall activity, and social interactions with other peers and adults. The behavioral categories range from basic positive mother-infant interactions of proximity, to negative interactions, such as aggression. Other categories recorded include noncontact and contact aggression, grooming, rejection, passivity, and any self-directed or anxious behavior exhibited from the infant (see Table 1 for behavior definitions).

Table 1

Behavioral Definitions

Behavior	Definitions
Approach by Infant	Infant moves toward mother, creating social contact with mother.
Approach by Mother	Mother moves toward infant, creating social contact with infant.
Contact Aggression	Performance of aggressive behaviors which include bites, slaps, any aggression that includes physical contact with the recipient.
Environmental Explore	Any active or attempted manual, oral, or pedal examination, exploration, or manipulation of the external environment.
Give groom mother/infant	Cleaning or grooming by the focal animal (mother or infant). Includes scratching, biting, licking, or rubbing, and occurs only between mother and infant.
Locomotion	Any self-induced change in location of self. Includes changes in location by means of walking, running, dropping from ceiling to floor, swinging across the cage (but not chain swinging), and bouncing, rolling, hopping on all fours, bouncing around the cage, and "displays." Also includes any movements across the substrate. Social behavior and locomotion are exclusive and when they occur simultaneously, Social is given precedence over locomotion, and if a motor pattern is repeated more than three times it is scored as Stereotypy.
Leave by Infant	Infant breaks social contact after being social with mother.
Leave by Mom	Mother breaks social contact after being social with infant.
Mutual Ventral	Infant is belly to belly with mother, on mother's nipple, or has arm around mother.
Mutual Break	Occurs when mother and infant stop being ventral, or belly-to-belly.
Noncontact Aggression	Performance of aggressive behaviors including aggressive chases and threats.
Passive	Absence of directed movement, social behaviors and environmental manipulation. Includes the occasional bouncing in place. No simultaneous scoreable social or non-social behaviors, except self-directed and self-mouthing

	behaviors and vocalizations.
Receive groom mother/infant	Animal of focus (mother or infant) receive cleaning or grooming from the other. Includes scratching, biting, licking, or rubbing. Grooming can only be between the mother and infant.
Receive Contact Aggression	Animal of focus is recipient of aggressive behaviors including bites, slaps and aggression that result in physical contact.
Receive Noncontact Aggression	Animal of focus is recipient of aggressive chases or threats.
Reject/Withdraw by Mom	Mother rejects approaches made by infant for mutual ventral contact. Also scored if there is mutual ventral contact and the mother attempts to break when the infant does not want to.
Self-Directed	Includes firm manual or pedal gripping of self, which is not a component of an ongoing behavior. Includes self-grooming and self-scratching, but not self-mouthing.
Self-Mouth	Includes sucking of self, not biting, at any bodily appendage.
Social Other	Animal of focus sitting, standing, locomoting, or lying within arm's reach other another animal. Precedence over locomotion. Not scored with Stereotypy or Stypic.
Social with Mother/Infant	Same as Social Other, except animal of focus is within arm's reach of mother/infant.
Social Play	Performance of any play behaviors including: initiating play by “play face,” wrestling (rough and tumble), chasing, tagging, swatting, bobbing, biting, pulling, lunging, mouthing, and responding positively to play from another animal. Still scored as Social Play if animal of focus is trying to initiate play with an unreciprocating partner. Implies social contact. Includes sexual play and mounting of another animal, whether appropriately or inappropriately oriented, with or without thrusting, mount attempts, rump presenting, and receiving a mount from another animal.

Stereo/Stypic	Stereotypy: any repetitive, patterned, and rhythmic locomotive movement, which is only scored following the third repetition of the motor act, then scored whenever it occurs. Stypic: any repetitive, non-locomotive action such as teeth picking, repetitive saluting, or strumming the mesh, which is also only scored following the third repetition of the act.
Vocalizations	Any vocal sound emitted by the subject. Includes coo, bark, screech, squeal, etc. Can be scored with any other behavior. Does not including coughing or sneezing sounds.

*****Unless otherwise indicated the behaviors are mutually exclusive.

Genotyping

Using standard extraction methods, deoxyribonucleic acid (DNA) was isolated from whole blood, collected from the femoral vein under ketamine anesthesia (15 mg/kg, IM). The rhesus serotonin transporter promoter region of both the short (388 bp) and long (419 bp) were amplified using primers (stpr5, 5'-GGCGTTGCCGCTCTGAATGC; intl, 5'-CAGGGGAG-ATCCTGGGAGGA) and polymerase chain reaction conditions described in Lesch et al. (1996). Amplicons were separated by gel electrophoresis and the short (388 bp) and long (419 bp) alleles of the rh5-HTTLPR were identified through ethidium bromide staining (Barr et al., 2004).

Cerebrospinal Fluid Procedure

Following a general anesthesia with ketamine (15 mg/kg) and a surgical prep, a cerebrospinal fluid (CSF) sample (1-2 mL) was obtained from the cisterna magna of each subject using a 22-gauge needle and a 5-cc syringe. Researchers recorded time to enter the monkeys' housing room, time until injection, and time until CSF and blood samples were drawn. The CSF samples were then quick-frozen and maintained in a –70*1* ultracold freezer. They were later assayed for 5-HIAA, HVA, and MHPG using high-performance liquid chromatography with electrochemical detection (Scheinin et al., 1983). All intra and interassay coefficients of variation were less than 10% (Higley et al., 1992; Mehlman et al., 1995). Because in humans CSF removal results in headaches in a small number of people, acetaminophen or Ketoprofen™ were administered prophylactically to all subjects to ameliorate potential post CSF discomfort (no subjects showed evidence of post CSF discomfort (Scheinin et al., 1983)). CSF 5-HIAA was measured on the following days: 7, 14, 30, 60, 90, 120, 150, 180 (roughly 6 months) and 187.

Data Analysis

All data were analyzed using a hierarchical linear mixed model comparing behavioral and physiological variables in adopted and non-adopted rhesus macaque infants. There are 145 infant monkeys included in this study, however, sample sizes for each of the hypotheses differs based on the availability of behavioral/physiological data from each monkey. Given the data organization, a hierarchical linear model was used to account for the organizational structure in the monkeys in which a cohort (n = 13) contains individual monkeys and each monkey has six observations. Specifically, by using a linear mixed model, both individual and cohort specific variations can be accounted for through random intercepts. Relevant explanatory variables were used to control for confounding effects (e.g. adoption, gender, and month). Analyses were conducted using Stata SE 11 (Statacorp LP, College Station, TX) and R (www.r-project.org). Also, to control for extremes or laboratory errors, any outliers in the behavioral scores were thrown out before starting analyses.

In the model, the behaviors and CSF serotonin metabolite count per day were analyzed as response variables and the following explanatory variables were coded: adopt (coded 1 = adopted, 0 = nonadopted), gender (coded 1 = female, 0 = male), month (coded 1 = first month, 2 = second month, ... 6 = sixth month), and genotype (coded 1 = long, 2 = short). The data were organized with repeated measures on each infant macaque and the infants were organized into cohorts. The equations (1-4) representing the model are as follows:

Observational level: $Y_{ijk} = \beta_{0ij} + \beta_{1ij}(adopt_{ijk}) + \beta_{2ij}(gender_{ijk}) + \beta_{3ij}(month_{ijk}) +$

$\beta_{4ij}(adopt_{ijk}*month_{ijk}) + \beta_{5ij}(adopt_{ijk}*infant\ genotype_{ijk}) + \beta_{6ij}(adopt_{ijk}*mother\ genotype_{ijk}) +$

$\beta_{7ij}(adopt_{ijk}*CSFday_{ijk}) + \varepsilon_{ijk}$ (1)

Individual level: $\beta_{0ij} = \beta_{00i} + \alpha_{0ij}$ (2)

Cohort level: $\beta_{00i} = \beta_{00} + \alpha_{00i}$ (3)

Overall: $Y_{ijk} = \beta_{00} + \alpha_{0ij} + \alpha_{00i} + \beta_{1ij}(adopt_{ijk}) + \beta_{2ij}(gender_{ijk}) + \beta_{3ij}(month_{ijk}) +$

$\beta_{4ij}(adopt_{ijk}*month_{ijk}) + \beta_{5ij}(adopt_{ijk}*infant\ genotype_{ijk}) + \beta_{6ij}(adopt_{ijk}*mother\ genotype_{ijk}) +$

$\beta_{7ij}(adopt_{ijk}*CSFday_{ijk}) + \varepsilon_{ijk}$ (4)

Where α_{0ij} and α_{00i} are the individual specific and cohort specific variations, and i = cohorts (1-8), j = individuals (1-n, n = # of individual monkeys), k = months (1-6). All reported results were tested at $p < .05$. Preliminary analyses report no differences between cohorts in any of the variables analyzed.

Results

Adoption Effect on Behavior

Hypothesis 1. Behavioral recordings for the first hypothesis were available from 42 adopted infant macaques and 80 nonadopted infant macaques. The behaviors analyzed in the first hypothesis include: Approach by infant, approach by mother, environmental exploration, locomotion, infant grooms mother, leave by infant, leave by mother, mutual ventral, mutual break, infant receives groom from mother, mother rejects or withdraws from infant, infant is social with mother, infant is social with others in social group, infant vocalizations, and social play; and their explanatory variables include adoption, month, and sex.

Main effects of adoption. Controlling for gender, month, and cohort, the following statistically significant main effects were found with adopted infants when compared to nonadopted infants (see Table 2): (a) Adopted infants completed 0.30 more approaches per 5-minute session to their mothers (see Figure 1), (b) adopted infants explored the environment 4.76 seconds more per 5-minute session, (c) adopted infants locomoted (i.e. walked, ran, change position) 2.85 seconds more per 5-minute session, (d) adopted infants completed 0.25 more withdrawals from their mothers per 5-minute session (see Figure 2), (e) adopted infants were held to their mother’s breast 13.73 seconds less per 5-minute session, (f) adopted infants were groomed by their mothers 5.30 seconds more per 5-minute session, and (g) adoptive mothers completed 0.12 more rejections of their infants per 5-minute session (see Figure 3).

Table 2

Summary of Adoption Effect on Behavior

	Adoption Variable		
Behavior	*Regression Coefficient*	*Std. Error*	*p*
Approach by Infant	0.30	0.11	.008
Approach by Mother	-0.02	0.05	.74
Contact Aggression	-0.001	0.003	.56
Explore Environment	4.76	1.68	.005
Infant grooms Mother	0.25	0.14	.07
Locomotion	2.85	0.95	.003
Leave by Infant	0.25	0.10	.02
Leave by Mother	-0.01	0.08	.88
Mutual Ventral	-13.73	5.21	.01
Mutual Break	-0.05	0.09	.57
Noncontact Aggression	0.01	0.003	.04
Passive	3.01	1.67	.07
Mother grooms Infant	5.30	2.52	.04
Receive Contact Aggression	0.02	0.01	.12
Receive Noncontact Aggression	0.02	0.01	.03
Reject/Withdraw by Mother	0.12	0.04	.007
Self-Directed	1.02	0.28	<.001
Social Other	-0.21	2.15	.92
Social with Mother/Infant	3.67	2.02	.07
Social Play	0.56	0.35	.10
Stereo-Stypic	0.02	0.05	.71
Vocalizations	0.19	0.51	.71

Average Approaches by Adopted and Nonadopted Infant to Mother across Months

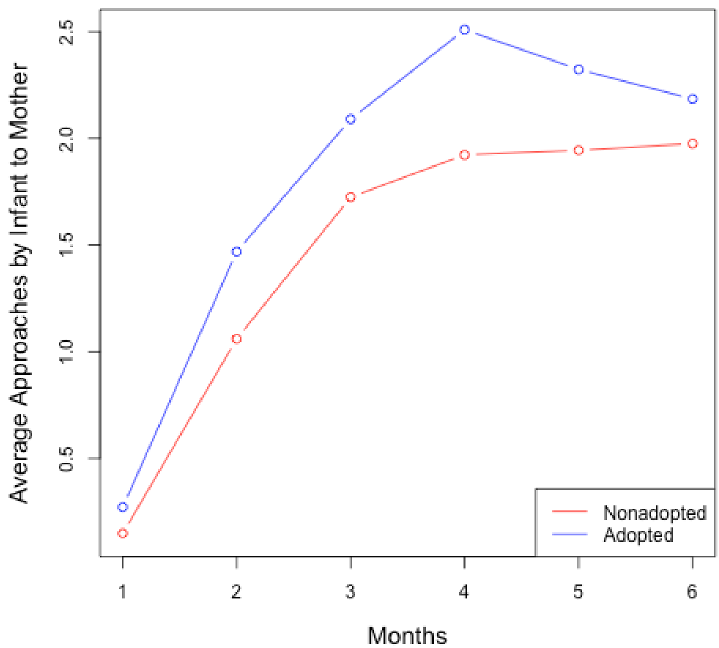

Figure 1. The effect of adoption on average approaches by infant to mother, $p = .008$. Adopted infants approached their mothers more frequently when compared to nonadopted infants.

Average Occurrences of Adopted and Nonadopted Infant Leaving Mother across Months

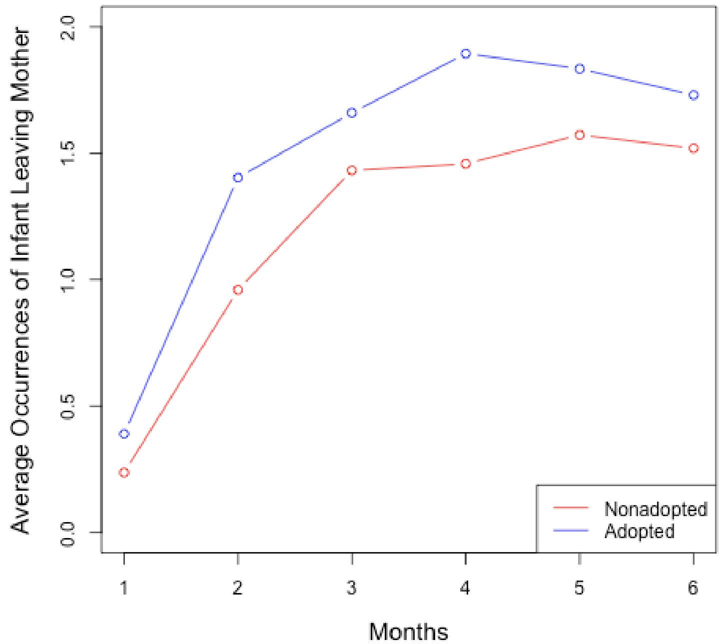

Figure 2. The effect of adoption on average occurrences of infant leaving mother, $p = .016$. Adopted infants left their mothers more frequently when compared to nonadopted infants.

Average Adopted and Nonadopted Infant Rejection by Mother across Months

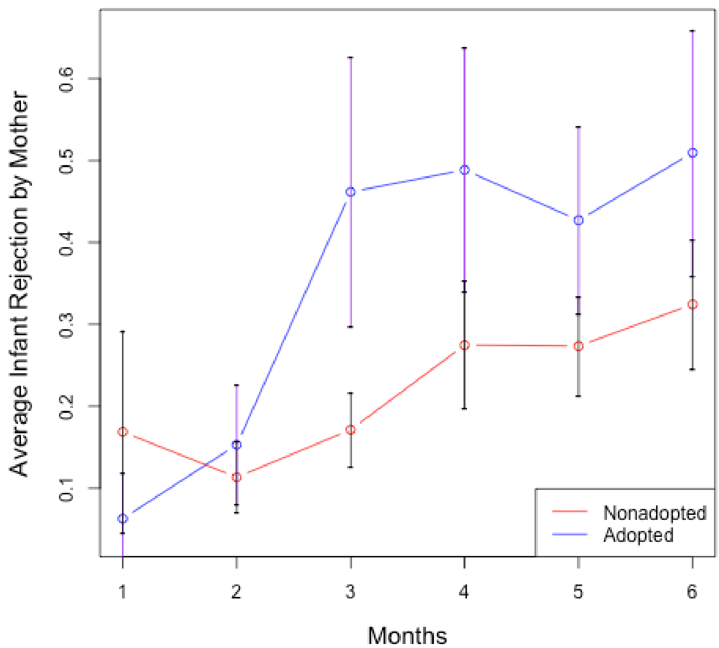

Figure 3. The effect of adoption on average infant rejection by mother across months, $p = .009$. Adopted infants were rejected by their mothers more frequently across months when compared to nonadopted infants. Post hoc analyses using Welch t tests show that at month three, $t(48) = -2.87$, $p = .01$, month four, $t(64) = -2.13$, $p = .04$, and month five, $t(65) = -1.99$, $p = .05$, are there significant differences between adopted and not adopted infants.

Adoption-by-month interactions. Controlling for gender and cohort, the following statistically significant interactions involving adoption and month were found with adopted infants when compared to nonadopted infants (see Table 3): (a) Adoptive mothers engaged in 0.05 more rejections of their infants per 5-minute session across months, and (b) interestingly, adopted infants engaged in 0.47 seconds more social play with their mothers per 5-minute session across months (see Figure 4).

Table 3

Summary of Adoption and Month Interaction Effect on Behavior

	Adoption*Month Interaction		
Behavior	*Regression Coefficient*	*Std. Error*	*p*
Approach by Infant	0.02	0.04	.71
Approach by Mother	-0.04	0.02	.06
Explore Environment	-0.24	0.73	.75
Infant grooms Mother	-0.07	0.07	.32
Locomotion	0.30	0.40	.45
Leave by Infant	-0.001	0.04	.97
Leave by Mother	-0.04	0.03	.17
Mutual Ventral	0.43	2.26	.85
Mutual Break	-0.05	0.04	.17
Noncontact Aggression	0.00	0.002	.99
Passive	-0.02	0.64	.98
Mother grooms Infant	-1.00	0.71	.16
Receive Contact Aggression	0.01	0.01	.14
Receive Noncontact Aggression	0.01	0.01	.25
Reject/Withdraw by Mother	0.05	0.02	.009
Self-Directed	0.07	0.12	.59
Social Other	0.003	0.87	.99
Social with Mother/Infant	-1.44	0.93	.12
Social Play	0.47	0.18	.01
Stereo-Stypic	0.02	0.03	.40
Vocalizations	0.23	0.22	.30

Average Adopted and Nonadopted Infant Play across Months

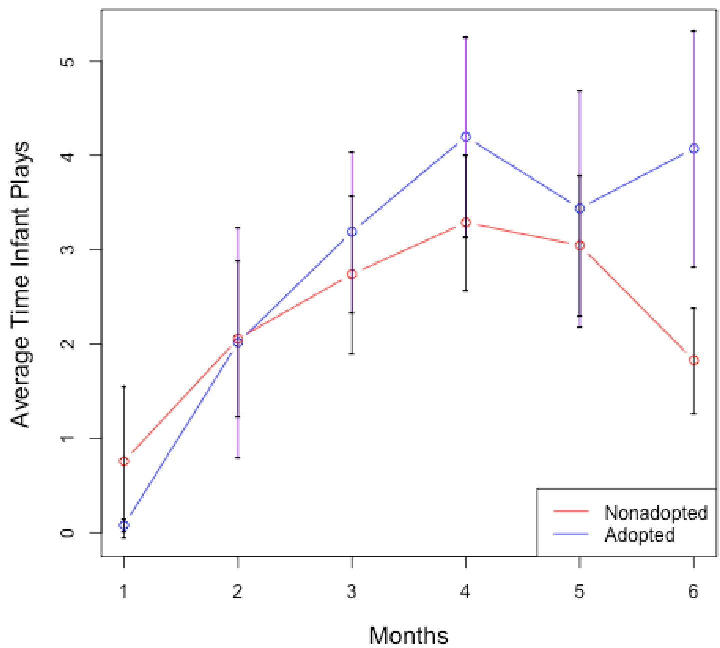

Figure 4. The effect of adoption on average infant play across months, *p* = .01. Adopted infants engaged in 0.47 more seconds in social play with their mothers per 5-minute session across months when compared to nonadopted infants. Post hoc analyses of the interaction using Welch t tests show that only at month six, *t*(58) = -2.74, *p* = .01, is there a significant difference between adopted and not adopted infants.

Hypothesis 2. Behavioral recording for the second hypothesis were available from 43 adopted infant macaques and 87 nonadopted infant macaques. The behaviors analyzed in the second hypothesis include: Infant giving contact aggression to group members, infant giving noncontact aggression to group members, infant receiving contact aggression from group members, infant receiving noncontact aggression from group members, overall aggression given, overall aggression received, and infant vocalizations.

Main effects of adoption. Controlling for gender, month, and cohort, the following statistically significant main effects were found with adopted infants when compared to nonadopted infants: (a) Adopted infants directed .01 more noncontact aggressive acts to other group members per 5-minute session, and (b) adopted infants received .02 more noncontact aggressive acts from other group members per 5-minute session (see Table 2).

Hypothesis 3. Behavioral recording for the third hypothesis were available from 43 adopted infant macaques and 86 nonadopted infant macaques. The behaviors analyzed in the third hypothesis include: Infant passivity, infant exhibiting self-directed behavior, infant exhibiting stereotypic and stypic behavior (i.e. repetitive, locomotive movement), and infant vocalizations.

Main effect of adoption. Controlling for gender, month, and cohort, the data indicate that adopted infants exhibited self-directed behavior 1.02 seconds longer per 5-minute session when compared to nonadopted infants (see Table 2 and Figure 5).

Average Adopted and Nonadopted Infant Self-Directed Behavior across Months

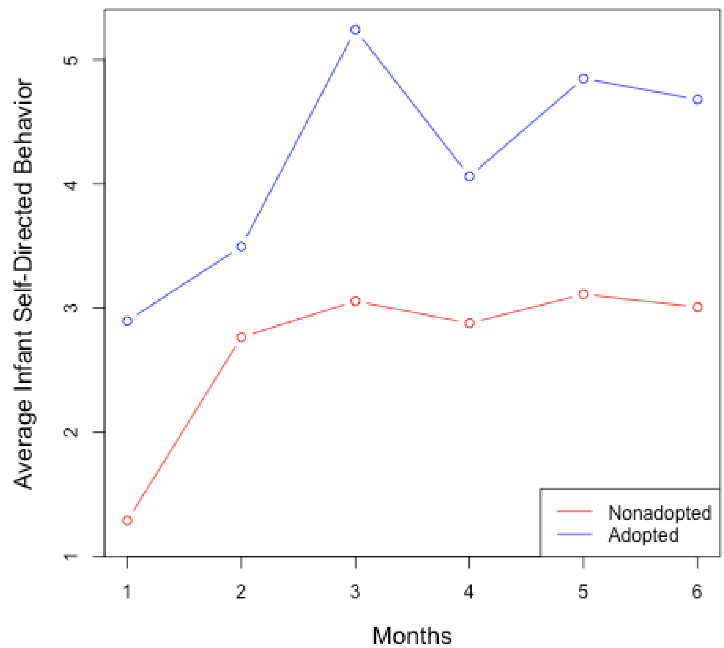

Figure 5. The effect of adoption on infant self-directed behavior (i.e. self-grooming, scratching, self-clasping, or hand-wringing), p <.001. The main effect showed that adopted infants exhibited self-directed behaviors more frequently when compared to nonadopted infants.

CSF Serotonin Count and Genotype

Hypothesis 4. Genotypes and cerebrospinal fluid (CSF) serotonin metabolite 5-hydroxyindoleacetic acid (5-HIAA) count for this analysis were available from 38 adopted infant macaques and their adoptive mothers and 102 nonadopted infant macaques and their biological mothers.

Main effect of adoption. Controlling for infant and mother HTTLPR genotype and gender, the data indicate that adopted infants show 66.55 lower 5-HIAA per day when compared to nonadopted infants (see Table 4 and Figure 6). There was no main effect for genotype.

Table 4

*Summary of Adoption, Infant HTTLPR Genotype, Mother HTTLPR Genotype, Day, Gender, and Adoption*Month Interaction Effect on CSF Serotonin (5-HIAA) Metabolite Count*

	CSF 5-HIAA		
Explanatory Variables	*Regression Coefficient*	*Std. Error*	*p*
Adoption	-66.55	22.14	.003
Infant HTTLPR Genotype	-13.70	16.06	.39
Mother HTTLPR Genotype	3.02	21.34	.89
Day	-3.34	0.08	<.001
Gender	7.87	15.24	.61
Adoption*Infant Genotype Interaction	21.63	34.56	.53
Adoption*Mother Genotype Interaction	34.60	43.18	.42
Adoption*Day Interaction	0.51	0.15	.001

Average CSF 5-HIAA Concentration in Adopted and Nonadopted Infants across Days

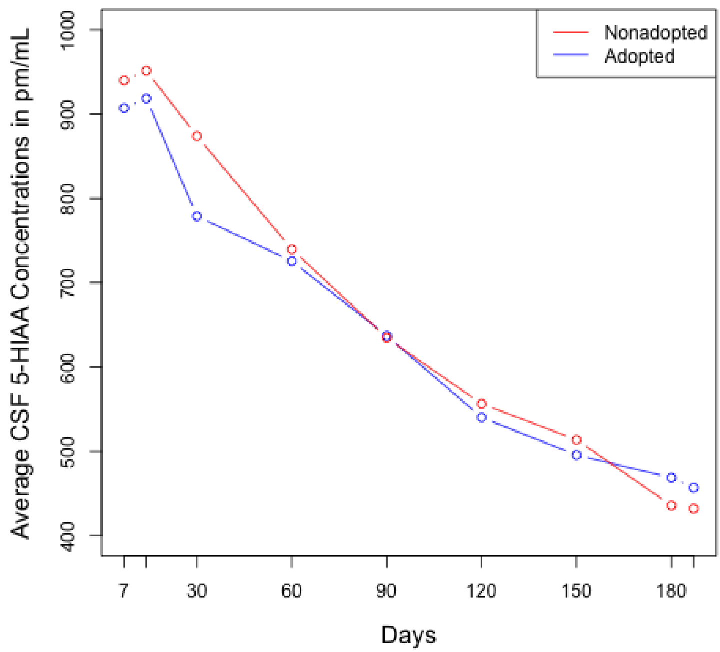

Figure 6. The effect of adoption on number of serotonin (5-HIAA) metabolites (measured in picomoles/milliliter) in infants, p = .003. The main effect of rearing showed that adopted infants have significantly less CSF 5-HIAA when compared to nonadopted infants. The graph demonstrates that CSF 5-HIAA difference between adopted infants at different days is not necessarily homogenous across months. Post hoc analyses of the interaction using Welch t tests show that only at day 30, $t(64) = 3.09$, p = .003, is there a significant difference between adopted and not adopted infants.

Discussion

To the extent that the results generalize to humans they provide behavioral and physiological clues as to why differences exist between adopted and nonadopted children. Such findings may be important additions to adoption literature. The hypotheses were largely supported by the data results. There are significant behavior differences between adopted and nonadopted rhesus macaque infants, indicating that when compared to infants reared by their biological mothers, adopted infants are more responsible for maintaining the relationship with their mothers, are rejected more frequently by their mothers, and direct to and receive more noncontact aggression from other group members. Adopted infants appear to be higher in anxiety, as measured by more self-directed behaviors (i.e. self-grooming, scratching) when compared with nonadopted infants. Also, there are significant physiological effects between adopted and nonadopted rhesus macaque infants' CSF serotonin (5-HIAA) metabolites, suggesting that adoption—at least in rhesus monkeys—may alter central nervous system function.

Adoptive Mother-Infant Relationship

It was hypothesized that (1) adopted infants would experience more conflict with their mother as a result of differing temperaments between the mother and infant. Moreover, because of the conflict, the infant would be more responsible for maintaining the relationship with their mother when compared to nonadopted infants. This hypothesis was largely supported by the data. Adopted infants were rejected more frequently by their mothers when compared to nonadopted infants, consistent with an interpretation that there was increased conflict between the adoptive mother and infant. This is consistent with research on abusive rhesus macaque mothers, who when compared with nonabusive mothers exhibited high rates of rejection

(McCormick, Sanchez, Bardi, & Maestripieri, 2006). According to Hinde, increasing rates of mother rejection with infant age is normal behavior for all mother-reared infants after the first few months of life (Hinde & Atkinson, 1970); however, this study shows adopted infants are consistently rejected more than nonadopted infants including the first few months of life. Rejections at such an early age may explain in part the increased anxiety seen in the adopted infants.

Additionally, adopted infants withdraw from their mothers more and spend less time being held by their mothers per 5-minute session when compared to nonadopted infants, which suggests a reflection on the adoptive mother-infant attachment. As described by Ainsworth (1978), secure attachment is also characterized by infant preferring mother (i.e. primary caregiver) to strangers and reliably utilizing mother as a secure base from whom they derive security and reduced arousal. As observed in this study, adopted infants complete more approaches to their mothers per 5-minute session, are more locomotive, engage longer in social play, and explore the environment for longer periods of time when compared to nonadopted infants. This trend is significantly different from nonadopted infants, and suggests that although there is increased conflict, the adopted infants still behave in a similar fashion to Ainsworth's (1978) description of a secure attachment. Also, adopted infants engage in more social play than nonadopted infants which is indicative of positive mental health (Thomas & Chess, 1977). This increased independence is not unlike what is seen in some human cultures, where independence is valued and children are allowed if not pushed to solve challenges with minimal parental support (Lamb, 1987).

Also consistent with secure attachment described by Ainsworth (1978) and Hinde and Spencer-Booth (1967), the adopted infants were also groomed for longer periods of time by their mothers when compared to nonadopted infants. The behavior of adoptive mothers suggests a secure attachment with their adopted infant, as well as reconciliation with the infant from a conflictual relationship. The results are consistent with studies of human mothers who adapt their behavior according to their infants' temperament and fit with early observations by Hinde and Spencer-Booth (1967), who noted that rhesus monkey mothers typically adapt their behavior to fit the developmental stage and temperament of the infant. This is also consistent with temperament theory which suggests the responsibility of mothers to exert more effort to be sensitive to their adopted infants' temperaments (Thomas & Chess, 1977), as well as adoption studies that suggest adopted children require more effort (Nickman et al., 2005; Wegar, 1995). It additionally suggests that evolution has favored a greater variety of developmental outcomes than one may have expected from Bowlby's (1953) predictions of normal mother-infant secure attachment interactions.

As a consequence of higher rejection rates and less spatial proximity to their mothers, it was hypothesized that (2) adopted infants would relate to other members in their social group with more negative interactions, such as aggression. This hypothesis was supported in that adopted infants both received and directed more noncontact aggression per 5-minute session to other social group members when compared to nonadopted infants. This is consistent with research by Nickman et al., (2005) in that adopted children "act out" more frequently as reported by adoptive mothers when compared to nonadopted children. Additionally, these high rates of mother rejection of their adopted infant from birth is inconsistent with normal mother rejection trends (Hinde & Atkinson, 1970), resulting in adopted infant "acting out", or expressing negative behavior (i.e. non-contact aggression) to other social group members. The higher rates of noncontact aggression may also be a result of the adopted infants' higher arousal (Harlow &

Zimmerman, 1958) because they are rejected more often and less able to use their mother as a secure base, and therefore relating to other social group members with more noncontact aggression. Alternatively, it may reflect that as the immature infant is independent of its mother, the infant may have a higher potential for negative interactions with other social group members that result in aggression.

Also as a consequence of high rejection rates, it was hypothesized that (3) adopted infants would exhibit more anxiety-related behaviors when compared to nonadopted infants. Higher rates of anxiety—such as self-directed behavior (i.e. self-grooming, scratching, self-clasping, or hand-wringing)—in the adopted infants largely supports this hypothesis. Adopted infants exhibited self-directed behaviors for longer periods of time when compared to nonadopted infants. This is not consistent with previous literature on rhesus macaque adoptions that found no differences between adopted and nonadopted infants (Champoux et al., 1995), and suggests that adopted infants' higher anxiety (i.e. self-directed behavior) is a result of the adoptive mothers' consistently higher rejection rate as well as the responsibility of the adopted infant to maintain the relationship with their mother (Hinde & Atkinson, 1970). This may also relate to the lack of arousal reduction (Harlow & Zimmerman, 1958) seen in adopted infants, who express more anxiety when compared to nonadopted infants who receive arousal reduction more reliably from their mothers. Alternatively, it may reflect the challenges felt by the immature infant in response to the larger social group.

Adopted Infant CSF Serotonin Count

As established in the literature, the serotonin transporter genotype is environmentally dependent and susceptible to stress. This finding lead to the hypothesis (4) that the adopted infants' genotypes would show a GxE interaction—i.e. as a consequence of high levels of rejection, monkeys with the short, less efficient genotype would produce less serotonin when compared to nonadopted infants. Although there is no observable serotonin transporter genotype effect accounted for in the data, the serotonin neurotransmission was affected by adoption in rhesus macaque infants. This is consistent with studies that have shown neurotransmission changes in response to early rearing experiences (Maestripieri et al., 2007; Bennett et al., 2002; Barr et al., 2003; Higley et al., 1993). Specifically, this data supports previous literature showing adopted infants who received higher rates of rejection had lower CSF 5-HIAA concentrations in comparison to infants less rejected (Maestripieri et al., 2007).

Conclusion

The data indicates that mother-infant temperament and attachment are significantly affected by adoption, although the effects are not entirely detrimental. The data suggests greater risk for anxiety and aggression in the adopted infants. On the other hand while biologically adoptive mothers and infants may on average be more likely to have differing temperaments, it was observed that mothers spend more time on average grooming their adopted infants when compared to nonadopted infants and they show evidence of an overall secure attachment bond. As mentioned by Thomas and Chess (1977), adoptive mothers must exert more effort than nonadoptive mothers to be sensitive to their infants' behaviors and needs. This is also congruent with Hinde and Spencer-Booth's remarks on attachment (1967). Also, adoption has a negative effect on the regulation of serotonin in the infant, which is likely an effect of early rearing experiences.

While considering the implications of this study, there are limitations to note. First, the research was conducted on nonhuman primates. Although rhesus macaques are genetically and behaviorally similar to humans (Bennett et al., 2002), they are not humans, and do not share all the complexities of human behavior and physiology. Thus there should be caution in making generalizations from monkeys to humans. Second, important missing genotype data (not all infant and mother genotypes were available for this study) lead to a small sample size for this set of analyses, which might have left the analyses underpowered to detect the genotypic main effects and interactions with adoption. Third, these findings are limited to the first 6 months of life, which are equivalent to about 2-3 years of development in humans, and essentially limits our knowledge of the long-term ramifications of adoption. Research on adoption, with specific address to temperament and attachment, might gather longitudinal data for all the childhood and adolescent years in order to have a more complete understanding of adoptive effects.

However, with these limitations in mind, the results of this study still present significant findings to adoption literature. Continuing research in adoption using longitudinal data is essential to understand adoptive mother-infant relationships in both humans and nonhuman primates.

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