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Quantitative Genetics of Response to Novelty and Other Stimuli by Infant Rhesus Macaques (*Macaca mulatta*) Across Three Behavioral Assessments

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Abstract

Primate behavior is influenced by both heritable factors and environmental experience during development. Previous studies of rhesus macaques (*Macaca mulatta*) examined the effects of genetic variation on expressed behavior and related neurobiological traits (heritability and/or genetic association) using a variety of study designs. Most of these prior studies examined genetic effects on the behavior of adults or adolescent rhesus macaques, not in young macaques early in development. To assess environmental and additive genetic variation in behavioral reactivity and response to novelty among infants, we investigated a range of behavioral traits in a large number ($N = 428$) of pedigreed infants born and housed in large outdoor corrals at the Oregon National Primate Research Center (ONPRC). We recorded the behavior of each subject during a series of brief tests, involving exposure of each infant to a novel environment, to a social threat without the mother present, and to a novel environment with its mother present but sedated. We found significant heritability (h^2) for willingness to move away from the mother and explore a novel environment ($h^2 = 0.25 \pm 0.13$; $P = 0.003$). The infants also exhibited a range of heritable behavioral reactions to separation stress or to threat when the mother was not present ($h^2 = 0.23 \pm 0.13$ – 0.24 ± 0.15 , $P < 0.01$). We observed no evidence of maternal environmental effects on these

traits. Our results extend knowledge of genetic influences on temperament and reactivity in nonhuman primates by demonstrating that several measures of behavioral reactivity among infant rhesus macaques are heritable.

Keywords

Anxiety; Heritability; Maternal environmental effects; Temperament

Introduction

A number of factors influence the differences in behavior observed among individuals within a primate species. Past research clearly demonstrates that individual experience can affect behavioral development in nonhuman primates, and that the early developmental environment can have enduring, even lifelong, consequences (Fairbanks and McGuire 1988; Rommeck *et al.* 2011; Sanchez *et al.* 2001; Suomi 1997; Weaver *et al.* 2004). The nature of the maternal–infant relationship is one particularly important environmental variable that affects early development (Altmann 2001; Bonnie *et al.* 2012; MacKinnon *et al.* 2007; Nishida 1988). In addition, the position of an individual adult animal within the network of social and kinship relationships inherent in all nonhuman primate social systems will influence aspects of that individual's behavior (Beehner *et al.* 2005; Engh *et al.* 2006; Sade 1967; Silk *et al.* 2010; van de Waal *et al.* 2013).

In comparison with social factors or developmental experience, the influence of genetic variation on individual differences in behavior has received less attention. Studies have documented additive genetic heritability, i.e., narrow sense heritability, for various behavioral traits among African green monkeys (*Chlorocebus sabaeus*: Fairbanks *et al.* 2004), chimpanzees (*Pan troglodytes*: Weiss *et al.* 2000), and rhesus macaques (Oler *et al.* 2010; Rogers *et al.* 2008). Other studies have identified a genetic association between particular DNA sequence polymorphisms and specific aspects of behavior (Bailey *et al.* 2007; Barr *et al.* 2003, 2008, 2009; Embree *et al.* 2013; Karere *et al.* 2009; Kinnally *et al.* 2008, 2010; Lindell *et al.* 2012; Rogers *et al.* 2013; Spinelli *et al.* 2012; Vallender *et al.* 2008). Further, specific behavioral traits related to temperament, behavioral reactivity, and impulsivity have shown sex differences and genotype $\times$ sex interactions (Barr *et al.* 2004; Fairbanks *et al.* 2004; Rogers *et al.* 2008). A thorough understanding of how both environmental and genetic processes influence behavior is important for a number of reasons, including our understanding of the biological mechanisms that govern behavioral development (both normal and pathological) and the analysis of behavioral evolution across species. Only behavioral traits with significant genetic heritability are subject to evolution through natural selection.

Rhesus macaques (*Macaca mulatta*) have proven to be a valuable model species for studies of the causes and consequences of individual behavioral variation. Rhesus macaques display robust adaptability to different environmental circumstances (Kessler and Berard 1989; Richard *et al.* 1989; Suomi 1997). The behavioral repertoire of rhesus macaques has been studied extensively and in detail (Capitanio and Widaman 2005; Sade 1967; Symons 1974; Thierry 2011). Evidence for genetic effects on temperament and other aspects of individual variation in behavior among rhesus macaques is growing steadily (Brent *et al.* 2013; Champoux *et al.* 1994; Sullivan *et al.* 2011).

However, though the amount of information concerning behavioral genetics in macaques and other nonhuman primates is increasing, aspects of this field have not received adequate attention. One such topic is the potential for differences in genetic effects across the

lifespan. Prior work concerning rhesus macaques has identified significant genetic effects on the behavior of adult (Barr *et al.* 2008; Kinnally *et al.* 2008) and juvenile animals (Barr *et al.* 2003; Oler *et al.* 2010; Rogers *et al.* 2008, 2013), but not among infants. Studies of human behavioral genetics show that temperament and other components of behavioral variation exhibit significant heritability at many ages, including infants (Plomin *et al.* 1993; Saudino 2005). In addition, genetic effects on human behavior change across the lifespan (Anokhin *et al.* 2009; Heiman *et al.* 2004; Plomin *et al.* 1993). Given this evidence for genetic effects on the behavior of human infants and the existing data showing that the behavior of rhesus macaques is influenced both by early developmental experience and by gene–environment interaction (Barr *et al.* 2009; Kinnally *et al.* 2010; Lindell *et al.* 2010, 2012), there is strong justification for investigating the genetic basis of individual variation in behavior among infant rhesus macaques.

For these reasons, we designed a study to estimate the additive genetic effects on, i.e., narrow sense heritability of, behavioral variation among rhesus macaques aged <6 mo. By examining infant rhesus macaques born into a multigeneration pedigree and raised in large species-typical social groups, we intended to quantify genetic and sex-specific influences on behavioral reactivity while testing and controlling for maternal environmental effects. A preliminary study had provided initial evidence for additive genetic variation in behavior among infant rhesus from the Oregon National Primate Research Center (ONPRC), but that study was limited by small sample size (Williamson *et al.* 2003). In the current study, we challenged 428 infant rhesus macaques with a series of standardized behavioral tests designed to measure differences in reactivity to various circumstances and stimuli. We used the known kinship relationships among animals to estimate the relationship between genetic variation and phenotypic variation and simultaneously estimated the effect of maternal environment. We predicted that specific behavioral traits would show significant heritability, and also tested for possible differences in genetic effects between the sexes.

Methods

Subjects

The study population consisted of 428 pedigreed infant Indian-origin rhesus macaques, *Macaca mulatta* (204 males, 224 females). Oregon National Primate Research Center (Beaverton, OR) maintained and bred the macaques used in this study. Macaques born between March 2003 and August 2007 underwent behavioral testing during the spring and summer as part of the annual capture and examination of all individuals in these corrals. We tested macaques only once in infancy for each behavioral test.

Age Estimation for Subjects

We tested only subjects that were between the ages of 40 and 158 d. Exact birth dates for individuals are not available because they were born in the outdoor breeding corrals, where complete demographic counts are not performed daily. However, we used dental eruption data and body weights to estimate the age of each individual at the time it underwent behavioral testing. We assigned ages based on the dental eruption schedule published by McNamara, Foster, and Rosenstein (1977). We determined ages of individuals in which all first molars had not yet erupted by specific tooth eruption. The majority of individuals (61%) possessed all four first molars erupted, but had no second molars present. The mean times to reach these two developmental milestones are 77 ± 18 d (complete set of first molars erupted) and 140 ± 23 d (initial eruption of second molar). We further subdivided this group to facilitate more precise aging. We assigned individuals with body masses below the median value for mass within this age-interval group the age of 93 d, as this is the midpoint between 77 and 109 d (109 is the midpoint between the outer boundaries of the full

interval, 77 and 140 d). We assigned individuals in the 77- to 140-d age interval with body mass above the median for the group the age of 124 d (midpoint between 109 and 140 d). We designated individuals with one or more second molars erupted at age 158 d.

Pedigree Relationships

The corral breeding groups consisted of multiple adult males and multiple adult females, so the parentage of individual infants was not known with certainty. To identify the sire and confirm the dam for each infant, we genotyped all infants and all potential parents for 16 microsatellite polymorphisms (Rogers *et al.* 2005) and used genotype-based exclusion methods using the PedSys software package (parents tool) (Texas Biomedical Research Institute, San Antonio, TX) to determine the sire and dam for each infant study subject. Initially, we used behavioral observations prior to capture to identify dams, and these records were largely but not entirely confirmed by genetic testing. Using the results from microsatellite analysis, we constructed a pedigree that links 428 infant study subjects into multiple generation pedigrees suitable for quantitative genetic (heritability) analysis. The complete data set of study subjects plus linking parents and ancestors consists of 928 individuals in 9 families. There are 50 sires with a mean of 21 ± 10 progeny and 265 dams with a mean of 4 ± 2 progeny. There were two major sires in the population, one with 35 and the other with 52 progeny.

Behavioral Testing: Free Play Test

The Free Play (FP) test measures exploratory behavior in a novel environment (Williamson *et al.* 2003). The infant macaque is placed in a playroom containing unfamiliar items, i.e., children's toys, climbing structures, etc., for 35 min. To allow for the mother's physical presence while ensuring that the mother could not influence the behavior of the infant, we sedated the infant's mother with ketamine (10–20 mg/kg, I.M.; Ketaset, Fort Dodge Animal Health, Fort Dodge, IA) and placed her in a seated position in an infant car seat in the corner of the playroom. Observations indicated that infants typically use their mother as a secure base in a manner similar to what is seen in the home cage. Recordings of each infant occurred through a one-way window at 0–5 min (immediately after it was placed in the playroom; period 1), at 15–20 min (period 2), and at 30–35 min (period 3). We scored behavior recorded on videotapes using the computer program Observer (Noldus, The Netherlands). Behaviors scored in this test include movement, time spent active, time spent playing with toys, vocalizations, initial latency to leave mother, distance from mother, and amount of time spent away from the mother.

Behavioral Testing: Human Intruder Test

Ned Kalin originally developed the Human Intruder Test (HIT; Kalin and Shelton, 1989) to assess behavioral responsiveness among rhesus macaques to either a threatening or a nonthreatening stimulus. Goldsmith and collaborators modified this test for use in children (Goldsmith 1990). Williamson *et al.* (2003) describe the modification of the HIT that we used in this study. In the HIT, we brought macaques from the FP test and placed them alone in a standard monkey cage in a novel room. After a 10-min period of acclimation to avoid confounding the response to the novel human interaction with the novel environment, they were videotaped from behind a blind. Testing began with a 10-min control period with no human present (designated the alone-1 period). The macaques were then exposed to two 2-min periods with a human intruder (always a person whom they had never seen before), who stood *ca.* 0.3 m from the cage. In the first human intruder period (Profile), the intruder stood with his or her facial profile to the macaque, making no eye contact. In the second human intruder period (Stare), the intruder made continuous direct eye contact with the infant. Direct eye contact is a threatening stimulus for these macaques (Symons 1974). The Profile

and Stare periods were separated by a 2-min period in which the stranger left the room (alone-2). Finally, the intruder left the infant alone after the Stare period and researchers videotaped the infant for another 2 min (alone-3). Scored behaviors during all conditions of this test include vocalizations, exploration, movement, and reaction to stranger including freezing and fearful and threatening expressions by the study subject (Coleman *et al.* 2003; Williamson *et al.* 2003).

Behavioral Phenotypes

Based on an extensive search of the literature and our prior experience, we formulated an exhaustive ethogram of species-typical anxiety-like and reactive behaviors that was scored for each subject (Coleman *et al.* 2003; Williamson *et al.* 2003). In this analysis, we focus on a subset of these behaviors that characterize the subjects' distinct reactions to the three specific environmental challenges. Two of the behaviors are composite behaviors, comprising multiple individual behaviors assessed in the ethogram: Movement and Escape Behavior.

Phenotype Normalization

Sample sizes for individual phenotypes ranged from 346 to 404, due to missing data for specific tests in particular individuals. Pairwise interrater reliability was greater than $r = 0.85$. We tested each of our three phenotypes to determine whether they exhibited a Gaussian distribution of measured values (Electronic Supplementary Material Fig. 1). When a phenotype did not produce a Gaussian distribution, we attempted a series of transformations to achieve a closer fit to that expectation. Of the transformations attempted (log, inverse normal, box-cox), only the tobit (which can normalize censored data) resulted in a successful transformation. We normalized the three traits (Latency to Leave Mother, Movement, Escape Behavior, Table I) using the maximum likelihood tobit regression from the VGAM package (www.ats.ucla.edu/stat/r/dae/robit.htm) (Yee, 2010) in R (Ihaka *et al.* 1996). Tobit regression (Tobin, 1958) is appropriate when the observed phenotype distribution is censored, i.e., there appears to be an underlying distribution but a significant fraction of individual test scores fall at a boundary condition. In the cases of Latency to Leave Mother, Movement, and Escape behavior, this censoring occurs because some individuals scored at a boundary value, such as infants who never left their mothers, and were thus scored as 2100 s (the total duration of the test) for the Latency to Leave Mother behavior.

We used the following regression formula:

$$Y = \text{age} + \text{Breeding Group} + \text{Cohort} + \text{Date Temperament Test}, \quad (1)$$

where Y is the trait of interest being regressed, age is the estimated age based on dental eruption and weight data, Breeding Group is the breeding group in which the individual lived, Cohort is the year in which the individual was born, and Date Temperament Test is the date of behavioral testing. Residuals (μ) were then obtained from the tobit function. All residual distributions were checked visually by plotting data histograms as well as by QQ plot (Electronic Supplementary Material Fig. 2). Analyses were carried out using the residual values (Astemborski *et al.* 1985; Brown 1978). This approach retains and models all variance that is not explained by the specified environmental variables (breeding group, cohort, age, and date of temperament test) and successfully transforms the data into a distribution suitable for subsequent variance components analysis.

Calculation of Heritabilities

We calculated heritabilities using a variance components method (Almasy and Blangero 1998) implemented in SOLAR (Texas Biomedical Research Institute, San Antonio, TX). This approach uses the pairwise kinship values for all pairs of individuals in the data set, which are calculated based on the known pedigree. The model calculates the proportion of phenotypic variance attributable to additive genetic differences among animals as well as considering other variables. In this study we wished to distinguish phenotypic similarity among individuals that can be attributed to shared genes from similarity due to shared maternal environment, i.e., being raised by the same mother. We modeled maternal environmental effects by defining a random effects variable (maternal ID) scored 0 for pairs of infants with different mothers and 1 for pairs with the same mother. The full model is:

$$Y = \phi^2 * h_r^2 + I * e^2 + M * c^2, \quad (2)$$

where Y is the phenotypic variance of the trait, ϕ^2 represents the pedigree relationships matrix, h_r^2 is the additive genetic variance or heritability, I is the identity matrix, e^2 is the environmental variance, M is the pairwise maternal ID matrix (shared mother is 1, otherwise 0), and c^2 is the maternal environmental effect.

To determine the statistical significance of any given heritability estimate, the likelihood of a model in which individual pairwise differences in phenotype negatively correlate with pairwise kinship is compared with the alternative model in which there is no relationship between kinship and phenotype but where maternal environmental effects were considered. We compared four different models (Table IIA), the null model (model 1: no maternal environmental effects and no genetic effects), the polygenic model (model 2: no maternal environmental effects), the maternal environmental effects model (model 3: no genetic effects), and the full model (model 4) that incorporates both maternal environmental effects and additive genetic effects. To determine the significance of the maternal environmental effects, we compared models 2 and 4 using the log likelihood ratio test (D) (Table IIA). The log likelihood comparison of models 3 and 4 determines the significance of the additive genetic variation portion of the model (h^2). For traits that had been tobit-regressed, all covariates were accounted for in the calculation of the tobit regression (covariates are described in the regression formula above: age, breeding group, cohort, and date of the temperament testing), with the exception of sex, which was included as a covariate in the heritability analysis. We assessed sex-specific effects by analyzing each sex separately using the methods described previously, except that maternal effects were not modeled owing to the lack of significant maternal environmental effects in the full model.

Residuals for the variable Latency to Leave Mother deviated significantly from normality after regression using the tobit model (QQplot and histogram, Electronic Supplementary Material Fig. 2). Therefore, we also assessed the heritability of Latency to Leave Mother after transforming the censored values (latency equals 35 min) to 0, and all uncensored values to 1, and then analyzing this variable as a dichotomous trait (Break from Mother).

Ethical Note

This work was approved by the Institutional Animal Care and Use Committee (IACUC) for the Oregon National Primate Research Center. All behavioral testing was performed by scientific staff of the ONPRC, and all procedures were consistent with the policies of the International Primatological Society and standard practice in the United States.

Results

We found that several traits are significantly affected by genetic variation among the study subjects. When analyzed as a quantitative phenotype, Latency to Leave Mother, an indicator of “bold” temperament and reduced anxiety in the face of novelty, is significantly heritable ($h^2 = 0.254 \pm 0.147$, $P = 0.003$). The variable “Break from Mother,” which is a transformation of the quantitative variable Latency to Leave Mother into a dichotomous trait (broke contact with the mother at any time during the test vs. did not break contact) also shows significant genetic effects ($h^2 = 0.376 \pm 0.204$, $P = 0.007$). The measurement of Movement (locomotion and movement) during the Alone-1 component of the HIT exhibits significant heritability (the heritability is significantly higher than 0) ($h^2 = 0.304 \pm 0.153$, $P = 0.01$). During the Stare component of the HIT, Escape behavior also shows significant genetic influence ($h^2 = 0.240 \pm 0.154$, $P = 0.002$) (Table I).

In all of the aforementioned analyses, we tested for the effects of an infant’s maternal environment by determining whether the addition of maternal ID as a separate random effects variable improved the likelihood of the statistical model. In all cases, there was no statistically significant effect of this factor on individual differences in behavior (Table II).

Finally, we further examined genetic effects by analyzing males and females separately. Latency to Leave Mother is significantly heritable when analyzed in the male infant rhesus only, but not among the females (Table III). The heritability of Break from mother did not reach statistical significance in either sex tested separately. Both male and female infants exhibit significant genetic effects on Movement during the HIT in the Alone period, and Escape behavior is significantly heritable in female infant rhesus, but not among the males.

Discussion

Our results suggest that different individuals within this population are likely to express qualitatively or quantitatively different reactions to environmental and/or social challenges as a result of inherited genetic differences. This demonstration of genetic heritability for temperament and reactivity among very young rhesus macaques has implications for understanding a number of aspects of macaque behavioral development. For example, the results suggest that individual differences in play behavior, initiation of social interaction, and other aspects of infant activity may also be influenced by genetic variation (Jiang *et al.* 2012; Kinnally *et al.* 2010; Sullivan *et al.* 2011). This finding of genetic effects on infant temperament also has implications for understanding the dynamics of mother–infant relationships, as genetic predispositions among infants may influence the nature and progression of the dynamic mother–infant relationship.

We find no evidence for an effect of maternal environment (maternal ID) on individual differences in any of these measures of behavior. Similar results were obtained in a study of reactivity to unfamiliar conspecifics among African green monkeys (Fairbanks *et al.* 2004). This does not contradict the notion that maternal behavior and the mother–infant relationship are critical to behavioral development in rhesus macaques. Rather, our results indicate that within the population of macaques we studied here, individual differences in the genetic constitution of the focal infants exert much stronger influence on variation in subjects’ behavioral responses to these specific tests than does the maternal environment. In a different population of rhesus macaques, where the nature or variance in maternal behavior might be different than in this population, a different result might be obtained. For example, the lack of observed maternal effect among these subjects does not imply that nursery rearing rather than mother-rearing would have no effect on developmental outcomes (Suomi 1997; Vandeleest *et al.* 2011). We further note that in three out of four of the tests analyzed,

our estimated values for h^2 when maternal effects are included (model 4) are statistically significant but slightly lower than estimated values for h^2 when maternal effects are not included (model 2). Thus, though the effect of maternal environment did not reach statistical significance, there is some suggestion of nonzero effect.

Our results for sex-specific heritabilities should be interpreted cautiously and do not constitute strong evidence for differential sex-specific genetic effects on these traits. The positive results for one sex or the other in a given test do provide new information regarding genetic influences on behavior. However, lack of significant heritability in a given sex-specific test does not in this case justify concluding that there is no genetic effect on that subset of the population. This study includes a large total number of subjects, but the number of individuals in each sex-specific test is small enough to reduce statistical power. Therefore, failure to reach statistical significance in any single sex-specific test is not strong evidence against genetic effects.

It is important to consider the results for Latency to Leave Mother and Break from Mother together. The distribution of measured values for Latency to Leave Mother could not be transformed to a satisfactory normal distribution. The variance components model we used to estimate heritability assumes that traits are normally distributed, though the analysis is somewhat robust to violations of this assumption (Almasy and Blangero 1998). To determine unambiguously whether there are genetic effects on this behavior, we transformed the quantitative variable Latency to Leave Mother into the dichotomous variable Break with mother (scored as yes vs. no). The estimated heritability for Break with mother is statistically significant (Table IIB), indicating clearly that there are genetic effects on this behavior. The estimated heritability value for Latency to Leave Mother can be considered an initial provisional estimate for the heritability of this quantitative trait.

This study raises a number of questions for future research. Additional studies could be designed to determine whether the same genes that influence reactivity to these behavioral tests among infants also influence variation in older individuals. Although it is reasonable to assume that there is substantial overlap in the specific genes that affect variation in temperament or reactivity at different life stages, there may be genetic effects that differ pre- and post-puberty or before and after the completion of cortical development and establishment of the adult pattern of cortical interneuronal connectivity. Further, if environmental stimuli elicit different responses at different ages, then the proportion of total phenotypic variance attributed to genetic variation, i.e., the narrow sense heritability, of behavioral traits may change.

We anticipate that future studies will identify specific genes that influence these behavioral traits in infants. This will allow researchers to determine whether those genes affect behavioral variation through effects on brain structure and organization, through neurotransmitter function, or some other mechanism. Further, identification of causative genes will also open opportunities to determine whether these genes that influence variation among infant rhesus macaques are also significant contributors to individual variation within other species, including diverse branches of primate phylogeny (strepsirrhines, platyrrhines, apes, and humans). The results for the serotonin transporter and *CRHR1* loci certainly suggest that the same genes can influence variation in multiple species (Barr *et al.* 2003; Kinnally *et al.* 2008, 2010; Lindell *et al.* 2012; Rogers *et al.* 2013; Spinelli *et al.* 2012). At the same time, studies show that genetic variation present in one primate species may not be present in other species (Fawcett *et al.* 2011; Lesch *et al.* 1997; Street *et al.* 2007; Vallender *et al.* 2008), even among closely related taxa. Comparative studies of particular aspects of primate behavioral genetics will be a fertile area for further study.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Table I

Behavioral traits examined in this study

Behavior	Test	Definition
Latency to Leave Mother	Free Play	Time in seconds until the subject first moved out of contact with its mother
Break from Mother	Free Play	A dichotomous treatment of Latency to Leave Mother representing whether or not the infant left the mother
Movement	Alone–Human Intruder Test (Alone–HIT)	Percent of time in locomotion or other movement during the initial Alone component of the HIT, before the person enters the test room
Escape behavior	Stare–Human Intruder Test (Stare–HIT)	Total percent of time performing the following: locomotion while looking at the intruder (vigilant), nonvigilant locomotion, or attempting to avoid the intruder during the Stare component of the HIT

Comparison of models for behavioral reactivity in infant rhesus macaques housed at Oregon National Primate Research Center

Table IIA

Model	Log likelihood of model 1: null model	Log likelihood of model 2: polygenic model	Log likelihood of model 3: maternal environmental model	Log likelihood of model 4: polygenic plus maternal environmental model	Log likelihood test (D) of model 2 vs. model 4 (is maternal effect significant)	Log likelihood test (D) of model 3 vs. model 4 (is h^2 significant)
Latency to Leave Mother	-1065.66	-1061.45	-1064.51	-1061.44	0.012 (1)	6.140 (0.003)
Break from Mother	-223.72	-220.73	-223.71	-220.73	n/a	5.977 (0.007)
Escape behavior	-1341.9	-1338.94	-1339.00	-1338.02	0.292 (0.294)	5.217 (0.011)
Movement	-1250.6	-1242.35	-1247.23	-1241.69	1.333 (0.113)	11.094 (0.002)

P values are represented in parentheses.

Table IIB

Heritabilities and maternal environmental effects for behavioral reactivity in rhesus macaques in the ONPRC

	Model 2: h^2	Model 3: Maternal environmental effects	Model 4: h^2 and SE	Model 4: Maternal environmental effects and SE
Latency to Leave Mother	0.263 (0.003)	0.109 (1)	0.254 ± 0.147 (0.002)	0.009 ± 0.085 (1)
Break from Mother	0.376 (0.007)	0.024 (1)	0.376 ± 0.204 (0.007)	0 (1)
Escape Behavior	0.295 (0.0015)	0.132 (0.300)	0.240 ± 0.154 (0.007)	0.044 ± 0.082 (0.294)
Movement	0.425 (0.00003)	0.176 (0.115)	0.304 ± 0.153 (0.00002)	0.094 ± 0.080 (0.114)

P values are represented in parentheses.

Table III
Sex-specific heritabilities of behavior reactivity traits in Oregon rhesus macaque population

	Sex analyzed	N	Model 1: sporadic (null) model	Model 2: polygenic model	Log likelihood test (D) of model 1 vs. model 2 (is h^2 significant)	Model 2: h^2	Model 2: SE	P value for h^2 (same P value for D)
Latency to Leave Mother	Male	165	-590.93	-589.35	3.170	0.337	0.238	0.037
	Female	181	-644.23	-643.84	0.773	0.175	0.223	0.190
Break from Mother	Male	167	-109.62	-108.75	1.736	0.488	0.392	0.094
	Female	184	-115.43	-114.52	1.827	0.471	0.412	0.088
Escape Behavior	Male	194	-663.73	-662.57	2.319	0.304	0.231	0.064
	Female	210	-702.56	-700.74	3.650	0.353	0.252	0.028
Movement	Male	183	-584.73	-582.92	3.626	0.364	0.251	0.028
	Female	205	-650.78	-649.18	3.200	0.212	0.162	0.037

Parameters that passed a significance threshold of $P < 0.05$ are in boldface.