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Parental genetic contributions to neonatal temperament in a nonhuman primate (*Macaca mulatta*) model

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Abstract

Temperament is an individual's nature and is widely believed to have a heritable foundation. Few studies, however, have evaluated paternal and maternal contributions to the triadic dimensions of temperament. Rhesus monkeys are widely utilized to model genetic contributions to human development due to their close genetic-relatedness and common temperament structure, providing a powerful translational model for investigating paternal and maternal genetic influences on temperament. The temperament of rhesus monkey infants born to 19 different sires and 50 different dams was assessed during the first month of life by comparing the temperament of paternal or maternal half-siblings reared with their mothers in species-normative conditions or reared in a neonatal nursery. Factor scores from three dimensions of temperament were obtained (Orienting/Regulation, Negative Affectivity, and Surgency/Extraversion) and ANOVAs were used to assess genetic effects. For paternal half-siblings, results showed a statistically significant paternal contribution to Orienting/Regulation, Negative Affectivity, and Surgency/Extraversion factor scores. For maternal half-siblings, results showed a statistically significant contribution

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CONFLICT OF INTEREST
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to Orienting/Regulation factor scores. When parsed by early rearing condition, results showed a paternal contribution Orienting/Regulation, Negative Affectivity, and Surgency/Extraversion scores for paternal half-siblings reared in the neonatal nursery, while there was only a paternal contribution to Surgency/Extraversion for paternal half-siblings reared by their mothers. There was only a maternal contribution to Orienting/Regulation for maternal half-siblings reared by their mothers. These results show that paternal and maternal contributions to temperament vary by environmental context, and that mothers may environmentally buffer their infants from paternal contributions to their temperament.

Keywords

heritability; maternity; paternity; temperament; triadic structure

1 | INTRODUCTION

Temperament refers to the cluster of constitutional traits that underlie stable individual differences in emotional disposition and behavioral reactivity (Shiner et al., 2012). Mounting evidence suggests that temperament is related to a myriad of important developmental outcomes, including resilience (Kim et al., 2013), relationships (Brody et al., 1996; Gleason et al., 2005; Thomas & Chess, 1977), disorders and psychopathology (Mian et al., 2011; Paterson et al., 2019; Rettew & McKee, 2005), and externalizing behaviors (Clark et al., 2015; Davis et al., 2018; Reviewed by DeLisi & Vaughn, 2014; DeLisi & Vaughn, 2015; Mineo et al., 2018; Wood et al., 2019). Paternal and maternal genetic contributions to general temperament have been established, suggesting that temperament is moderately heritable (h^2 = 0.20–0.60) in humans (Fagnani et al., 2017; Planalp et al., 2017; Saudino, 2005; Shiner et al., 2012). Studies also suggest that temperament is subject to the unique genetic profile of the offspring and to environmental variation (Barker et al., 2011; Bornstein et al., 2019; Gagne et al., 2013; Lemery-Chalfant et al., 2013). Studies show that human temperament has a triadic structure with three latent factors: affective regulation (Orienting/Regulation, including duration of orienting to a stimulus, soothability, and cuddliness), reactivity (Negative Affect, including fear, sadness, and distress to limitations, for example, being confined to a place or position), and activity (Extraversion/Surgency, including smiling and laughter, activity level, and high intensity pleasure) (Braungart et al., 1992; DeSantis et al., 2011; Gartstein et al., 2013; Matheny Jr., 1980, 1983; Rothbart, 1981). Disentangling the paternal and maternal contributions to the heritability of each temperament dimension is an active area of study that may both inform the role that parental genetics plays in development and may elucidate whether certain latent temperament dimensions are more or less subject to environmental variation.

While parsing out direct maternal and paternal genetic contributions to infant temperament is a relatively new endeavor, studies indicate that there are associations between paternal and maternal traits and the three dimensions of infant temperament. For example, studies show positive correlations between paternal effortful control and infant Orienting/Regulation (Potapova et al., 2014) and between paternal extraversion and infant Surgency/Extraversion (Komsi et al., 2008; Potapova et al., 2014). Paternal Negative Affectivity is also positively correlated with infant Negative Affectivity (Potapova et al., 2014). Other studies show positive correlations between maternal effortful control and offspring Orienting/Regulation (Bridgett et al., 2011; Gartstein et al., 2013). In these studies, however, environmental influences cannot be ruled out because the parents lived with their offspring. Translational animal studies afford greater environmental control, including randomization of exposure to certain environmental influences. Furthermore, stringent protocols can be maintained when collecting behaviors in a laboratory, including those related to temperament. These, among other reasons, increase the utility of animal studies for investigating the impact of genetics on temperament.

Rhesus macaques (*Macaca mulatta*) are ideally suited for such an endeavor, as both human and rhesus macaque infants exhibit homologous temperament dimensions (Kay et al., 2010; Wood et al., 2020), likely as a result of shared common ancestry and genetic similarities (Gibbs et al., 2007). Rhesus macaques also provide a high degree of experimental control, including a long history of use in assessing the role of the early rearing environment on developmental outcomes. By randomly assigning rhesus monkey infants to early rearing conditions in which their mothers are absent (nursery-rearing; NR) or to conditions in which their mothers are present (mother-rearing; MR), researchers attempt determine the role that maternal environmental effects have on infant development. It is also possible to assess paternal genetic and environmental effects on infant development, as rheus monkey fathers do not demonstrate direct infant care in a species-typical fashion (Lindburg, 1971). Several studies suggest that certain elements of temperament in rhesus macaques are heritable (Brent et al., 2014; Stevenson-Hinde & Simpson, 1981), and the rhesus macaque model has been previously utilized to examine parental contributions to temperament (Fawcett et al., 2014; Kinnally et al., 2018; Maestripieri, 2003; Stevenson-Hinde & Simpson, 1981; Sullivan et al., 2011; Williamson et al., 2003).

The current study assesses maternal and paternal genetic contributions to the triadic structure of infant temperament in a large number of infants. Infants were randomly assigned to MR or NR conditions and their temperament was assessed using the widely used and well-validated Infant Behavior Assessment Scale (Paukner et al., 2020). Infants were grouped as maternal or paternal half-siblings to assess paternal and maternal genetic contributions to the three dimensions of temperament identified in human and rhesus monkey infants. We hypothesized that there would be a sire and a dam effect for each of the temperament dimensions for maternal and paternal half-siblings. Studies examining paternal and maternal genetic contributions to offspring temperament in rhesus monkeys may provide important insight to factors that contribute to human infant temperament. This line of experimental investigation into paternal and maternal genetic contributions to temperament is an important step toward elucidating the impact of parental genetic contributions to infant temperament development.

2 | METHODS & MATERIALS

2.1 | Subjects

Subjects were drawn from a sample of 612 rhesus macaque infants (287 females, 325 males) born and housed at the Laboratory of Comparative Ethology, National Institute of Child

Health and Human Development in Poolesville, Maryland, USA between 1987 and 2006. As part of a larger research program, infants were randomly assigned to one of two rearing conditions at birth: MR ($n = 251$) infants were reared in conditions that approximated the natural social composition of rhesus monkeys, in groups with multiple adult females and other infants and two adult males; NR ($n = 361$) infants were separated from their mothers at birth and hand-reared in a neonatal nursery. Rearing procedures are described in detail elsewhere (see Schneider et al., 1991; Schneider & Suomi, 1992; Shannon et al., 2005). An extended comprehensive pedigree that dates back to the 1950 s was used to determine relatedness and outbreeding was assured by selecting unrelated females and males for each social group. Paternity was established by genotyping infants at a minimum of 7 microsatellite loci. All procedures were conducted in compliance with the Animal Care and Use Committee of the National Institutes of Health and in compliance with the US National Research Council's Guide for the Care and Use of Laboratory Animals.

2.2 | Measures

All subjects were assessed using the Infant Behavioral Assessment Scale (IBAS), a widely used standardized test for assessing temperament in rhesus monkeys. The IBAS is described in detail elsewhere (Schneider et al., 1991; Schneider & Suomi, 1992). Briefly, the IBAS was administered weekly for one month following birth. MR subjects were separated from their mothers and NR subjects were removed from the nursery for the testing period (20–30 min between 1000 and 1200 h). Technicians administering the test were trained by a senior scientist with a more than a decade of experience. Reliability checks were confirmed yearly to ensure that reliability was maintained (inter-rater reliability: $r > 0.90$).

2.3 | Temperament factor scores

Earlier multi-time point, multi-group confirmatory factor analyses (mmCFAs; Wood et al., 2020) confirmed the presence of three latent temperament dimensions: Orienting/Regulation, Negative Affectivity, and Surgency/Extraversion. The mmCFAs had weak invariance, indicating that, for each time point and rearing group, the IBAS items contributed to their respective latent factors to a similar degree. However, evidence of strong invariance was not achieved, suggesting that the factor scores are not directly comparable for each rearing group and time point. To allow for direct comparisons of the factor scores across rearing groups and time points, a series of partial strong invariance models were estimated. See Table 1 for definitions of the indicators included in each of the models. Maximum likelihood with robust standard errors estimates were used to test the fit of each model and model comparisons were made using chi-square difference tests, the Root Mean Square Error of Approximation (RMSEA), the Comparative Fit Index (CFI), and Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC). All mmCFAs and model comparisons were conducted in Mplus, version 8.

2.3.1 | Orienting/Regulation factor—For the Orienting/Regulation factor, the complete weak invariance model was superior to the complete strong invariance, indicating that the strong invariance across groups and time points was not fully achieved. To investigate whether a model with partial strong invariance might provide reasonable model fit and a basis for latent mean comparisons, several intermediate models were considered

(Table 2). At each occasion and in each group, four IBAS indicators for Orienting/ Regulation were measured (duration looking, visual follow, attention, and visual orienting; See Table 1 for definitions) and several modified strong invariance models were estimated, in which the intercept for each indicator was freed in turn. Model comparisons using the fit measures suggested that freeing the group and time point intercepts for the visual orientation and attention items provided the greatest fit improvements and that a model freeing the intercepts for both of these items provided a reasonably well-fitting model, although it was not superior to the weak invariance model. However, it is important to note that the AIC and BIC values of the partial strong invariance model are lower (thus, indicating a better fit; Kenny, 2015) than the weak invariance model. It should be noted that these comparisons do not attempt to achieve optimal partial strong invariance in terms of the smallest possible number of specific comparison parameters, rather they address strong invariance one full indicator at a time and the results are thus more stable and replicable.

2.3.2 | Negative affectivity factor—For the Negative Affectivity factor, the complete weak invariance model was superior to the complete strong invariance model, indicating that strong invariance across groups and time points was not fully achieved. To investigate whether a model with partial strong invariance might provide reasonable model fit and a basis for latent mean comparisons, several intermediate models were considered (Table 3). At each occasion and in each group, four IBAS indicators of Negative Affectivity were measured (irritability, soothability, predominate state, and response intensity; See Table 1 for definitions) and several modified strong invariance models were estimated, in which the intercept for each indicator was freed in turn. Model comparisons using the fit measures suggest that freeing the group and time point intercepts for the response intensity item provided the greatest fit improvement and a reasonably well-fitting model, although it was not superior to the weak invariance model. However, it is important to note that the BIC value of the partial strong invariance model was lower (thus, indicating a better fit; Kenny, 2015) than the weak invariance model. We note that these comparisons do not attempt to achieve optimal partial strong invariance in terms of the smallest possible number of specific comparison parameters, rather they address strong invariance one full indicator at a time and the results are thus more stable and replicable.

2.3.3 | Surgency/Extraversion factor—For the Surgency/Extraversion factor, even the configural model had poor fit, X^2 (148) = 895.812, CFI = 0.846, TLI = 0.751, RMSEA = 0.123, SRMR = 0.106. Two of the four indicators, motor activity, and passivity, had high factor loadings, but the factor loadings for the other two indicators, coordination and spontaneous locomotion, were quite low. Furthermore, the measurement errors were strongly correlated for these two items. There was a dramatic increase in model fit when residual covariances were added to the model. By adding just eight parameters (four time points for two groups), the model fit went from unacceptable to well-fitting (X^2 (140) = 273.487, CFI = 0.973, TLI = 0.953, RMSEA = 0.053, SRMR = 0.074). However, trying to repair a poorly fitting model by adding correlated errors seldom addresses the true source of the model misspecification. In this case, it appears that a single factor was insufficient to properly model the four indicators. Instead, two dimensions are necessary, one for motor activity and passivity and another for coordination and spontaneous locomotion. Although there is some concern with factors having only two indicators, treating all four items as measures of the same latent construct fails to achieve not only strong invariance but also fails in fitting the configural model. Thus, two of the items determined to be good indicators of Surgency/Extraversion, coordination and spontaneous locomotion (See Table 1 for definitions), were evaluated for invariance (Table 4). RMSEA values ≤0.08 were used as the threshold of acceptable fit for determining whether or not to reject the models (Browne & Cudeck, 1993). Due to the complexity of the models, CFI values ≥0.90 were regarded as indicative of good fit (Hu & Bentler, 1999). When comparing the two models, the ΔCFI was greater than ≤0.01, indicating a significant difference between the two models, and the AIC value was lower for the weak invariance model when compared to the strong invariance model. However, the BIC value for the strong invariance model was lower, providing evidence for a better fit (Kenny, 2015).

Factor scores for each of the factors from the partial strong invariance models for Orienting/ Regulation and Negative Affectivity and factor scores from the strong invariance model for Surgency/Extraversion were extracted and means for each factor score at each time point were utilized in subsequent analyses.

2.4 | Data analysis

Offspring were born to 165 different dams and 61 different sires. To assess the relationship between parentage and infant temperament, paternal half-siblings were grouped by sire and maternal half-siblings were grouped by dam. To ensure sufficient sample sizes per group, paternal or maternal half-siblings born to sires or dams with fewer than 4 offspring were excluded from analyses. In the paternal analyses, offspring from the same dam were randomly distributed across sire groupings and in the maternal analyses, offspring from the same sire were randomly distributed across dam groupings. Using these criteria, 144 subjects born to 19 different sires and 270 subjects born to 50 different dams were included in the analyses.

Paternal and maternal heritability of Orienting/Regulation, Negative Affectivity, and Surgency/Extraversion was calculated using a series of one-way ANOVAs. In each ANOVA, sire or dam was entered as the independent variable and a temperament factor score (Orienting/Regulation, Negative Affectivity, or Surgency/Extraversion) was entered as the dependent variable.

Heritability (h^2) of temperament was assessed using the ANOVA model that partials genetic and environmental contributions (Fuller & Thompson, 1960), using the following formula: h^2 = (MS Between/[MS Group + MS Between]) × degree of relatedness). As the present study assesses heritability among half-siblings, the degree of relatedness is 0.25. The ANOVA method makes no *a priori* predictions concerning which paternal or maternal infant groupings will differ, rather, a significant F ratio indicates that at least part of the variance is related to paternal or maternal genetic contributions to half-sibling phenotypes. All ANOVAs and heritability analyses were conducted in SPSS, version 26.

3 | RESULTS

Results from ANOVAs showed significant relationships between sire grouping and Orientation/Regulation ($F[18,125] = 1.98$, $p = 0.02$), Negative Affectivity ($F[18,125] = 2.72$, $p = 0.001$), and Surgency/Extraversion factor scores ($F[18,125] = 2.16$, $p = 0.007$) for paternal half-siblings. To assess whether the presence of the sire during the first 30 days of life impacted infant temperament, we repeated the ANOVAs and h^2 analyses separately for MR and NR paternal half-siblings. Results from these analyses showed that there was a significant relationship between sire grouping and Orienting/Regulation factor scores ($F[9,86] = 2.01$, $p = 0.05$), Negative Affectivity ($F[9,86] = 3.44$, $p = 0.001$), and Surgency/Extraversion factor scores ($F[9,86] = 2.40$, $p = 0.018$) for NR paternal half-siblings. Results also showed that there was a significant relationship between sire grouping and Surgency/Extraversion factor scores for MR paternal half-siblings ($F[4,45] = 2.85$, $p = 0.04$). The relationship between sire grouping and Orienting/Regulation factor scores for MR paternal half-siblings was not significant ($F[4,45] = 2.27$, $p = 0.08$), nor was the relationship between sire grouping and Negative Affectivity factor scores for MR paternal half-siblings ($F[4,25] = 0.37$, $p = 0.83$). See Table 5 for a summary of these analyses.

Results from ANOVAs showed a significant relationship between dam grouping and Orienting/Regulation factor scores for maternal half-siblings ($F[49,220] = 2.19$, $p < 0.0001$). However, the relationship between dam grouping and Negative Affectivity factor scores for maternal half-siblings was not significant ($F[49,220] = 0.96$, $p = 0.56$), and neither was the relationship between dam grouping and Surgency/Extraversion factor scores for maternal half-siblings ($F[49,220] = 0.97$, $p = 0.53$). To assess whether the presence of the dam during the first 30 days of life impacted infant temperament, we repeated the ANOVAs and h^2 analyses separately for MR and NR maternal half-siblings. Results from these analyses showed that the relationship between dam grouping and Orienting/Regulation factor scores for NR maternal half-siblings was not significant ($F[19,107] = 1.64$, $p = 0.06$), nor was the relationship between Negative Affectivity factor scores for NR maternal half-siblings ($F[19,107] = 0.82$, $p = 0.68$), nor was the relationship between Surgency/Extraversion factor scores for NR maternal half-siblings ($F[19,107] = 0.68$, $p = 0.83$). Results also showed that the relationship between dam grouping and Orienting/Regulation factor scores for MR maternal half-siblings was significant ($F[4,33] = 3.51$, $p = 0.02$). Results from these analyses showed that the relationship between dam grouping and Negative Affectivity factor scores for MR maternal half-siblings was not significant ($F[4,33] = 0.52$, $p = 0.72$), nor was the relationship between Surgency/Extraversion factor scores for MR maternal half-siblings ($F[4,33] = 2.06$, $p = .11$). See Table 5 for a summary of these analyses.

4 | DISCUSSION

The current study found partial support for the hypotheses that fathers and mothers have a direct genetic contribution to the three latent temperament dimensions. There were significant paternal heritable effects for all three of the temperament factors in the combined rearing condition sample. These findings replicated in the NR sample, where fathers and mothers were not present. For the MR subjects, there was only a paternal genetic effect on Surgency/Extraversion, while paternal genetic contributions were no longer significant for

Orienting/Regulation and Negative Affectivity. There were few significant maternal heritable effects on the latent temperament dimensions, with maternal genetic effects limited to the Orienting/Regulation factor in both the overall sample and in the MR group. In the NR sample, in which the fathers and mothers were not present, there was not a significant effect on Orienting/Regulation. These findings suggest that fathers and mothers have differential genetic contributions to the temperament of their offspring and that temperament is subject to environmental variation.

The significant paternal effects on the infant temperament factors are corroborated by other research suggesting that there are temperament similarities in human fathers and offspring (Babadagi et al., 2018; Komsi et al., 2008; Potapova et al., 2014). The current study, however, cannot dismiss the possibility that fathers of MR infants may have made some limited environmental contributions on their infant. Nevertheless, as male contributions to the infant environment in this species are largely indirect (Lindburg, 1971), it is not surprising that nursery rearing, which essentially removes all paternal environmental influences, did not attenuate paternal genetic effects on all three infant temperament dimensions. Alternatively, mothers exert a direct environmental influence on their infants that may attenuate paternal genetic effects in some aspects of infant temperament.

The significant maternal effects on Orienting/Regulation in both the combined rearing condition and the MR group are corroborated by research suggesting that there are temperament similarities in human mothers and their offspring (Bridgett et al., 2011; Elam et al., 2014; Gartstein et al., 2013; Hyde et al., 2016; Kusanagi et al., 2014; Waller et al., 2016) including significant positive relationships between human maternal effortful control and offspring Orienting/Regulation (Bridgett et al., 2011; Gartstein et al., 2013). It is surprising that there were no significant maternal effects for Negative Affectivity and Surgency/Extraversion. One parsimonious interpretation for this finding is that the maternal influences seen in the infants reared by their mothers are largely environmental in origin or that that the maternal genetic contributions are overshadowed by the impact of nursery rearing. Nursery-rearing is a potent environmental manipulation that may affect temperament, as it is associated with a plethora of developmental aberrations impacting the central nervous system (Bliss-Moreau et al., 2017; Sabatini et al., 2007; Sánchez et al., 1998), behavior (Bastian et al., 2003; Beauchamp & Gluck, 1988; Champoux et al., 1991; Corcoran et al., 2012), and temperament (Capitanio et al., 2006; Kay et al., 2010; Wood et al., 2020).

It is important to note that this method of assessing maternal and paternal contributions to development assesses whether there is a sire or dam effect when half-siblings are grouped by sire or dam. While this method is useful for assessing whether knowing a parent's identity can inform offspring development, it does not parse out similarities in the genome between offspring and parent. Heritability is a measure of how well genetic variation can account for differences in phenotypic expression of a trait. Thus, phenotypic variation in infant temperament is accounted for by genetics and environment. This study attempts to assess direct paternal genetic and direct maternal genetic influences on infant temperament, but does not comment specifically on which genes are responsible for temperament variation or whether there is an interaction of genetics and environment on infant temperament variation.

This study provides several novel contributions to temperament research. Prior work performed by the authors of this study determined that early infant temperament in nonhuman primates is also composed of the triad of latent structures observed in human infants (Kay et al., 2010; Wood et al., 2020), facilitating research on the heritability of infant temperament using an evolutionarily close relative. Additionally, a nonhuman primate model investigating the direct paternal and maternal genetic contributions to infant temperament allows for improved environmental control, reducing error in heritability estimates. Subjects were reared in homogeneous rearing conditions, particularly in the NR condition and fathers have a reduced environmental contribution in rhesus monkeys. While both major aberrations in early development and the lack of paternal care may potentially limit the generalizations that can be derived for humans from studies utilizing a rhesus macaque model, this study is an important first step in examining and identifying paternal and maternal genetic contributions on the triadic structure of temperament, and suggests that fathers exert important genetic effects on the temperament of their offspring.

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DATA AVAILABILITY STATEMENT

The data that support these findings are available from the corresponding author upon reasonable request and with permissions from the National Institutes of Health.

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TABLE 1

IBAS items utilized in partial strong invariance analyses

Factor	Item	Definition
Orienting/Regulation	Duration looking	Length of looking at orienting items
	Visual following	Eyes following moving toy in both horizontal & vertical directions
	Attention	Examiner rating of attention
	Visual orienting	Eyes oriented toward toy (plastic Mickey Mouse face) held in four positions in infant's periphery
Negative Affectivity	Irritability	Amount of distress noted during testing
	Soothability (upset)	The frequency in which soothing attempts of examiner were necessary to calm the infant during testing
	Predominant state (agitation)	State of infant during testing
	Response intensity (fear or hostility)	Scored based on the quality of vocalizations during testing
Surgency/Extraversion	Coordination	Quality of movement
	Spontaneous locomotion (activity level)	Quality of locomotion

Note.: For interpretation purposes several items were relabeled (listed in parentheses) to better highlight their similar to human behaviors or to clarify their relationship to their respective factors.

TABLE 2

Weak, strong, and selected intermediate (partial strong) models for Orienting/Regulation

Models	X^2 (*df*)	RMSEA	CFI	AIC	BIC
Full weak invariance	272.192(169)	0.043	0.984	11393	12001
Full strong invariance	633.495(190)	0.084	0.930	11712	12226
Partial strong invariance					
Free intercept: Duration looking	608.221(183)	0.083	0.933	11701	12246
Free intercept: Visual follow	532.184(183)	0.076	0.945	11625	12170
Free intercept: Attention	494.860(183)	0.071	0.951	11587	12133
Free intercept: Visual orientation	466.881(183)	0.068	0.955	11560	12105
Free intercept: Visual orientation +attention	381.019(176)	0.058	0.969	11478	12054

Note: Maximum likelihood results. All results represent standardized solutions.

TABLE 3

Weak, strong, and selected intermediate (partial strong) models for Negative Affectivity.

Models	X^2 (*df*)	RMSEA	CFI	AIC	BIC
Full weak invariance	348.79(169)	0.056	0.976	8105	8714
Full strong invariance	448.71(190)	0.064	0.956	8207	8720
Partial strong invariance					
Free intercept: Irritability	464.253(183)	0.068	0.963	8193	8738
Free intercept: Soothability	459.837(183)	0.067	0.964	8189	8734
Free intercept: Predominant state	448.848(183)	0.066	0.965	8178	8723
Free intercept: Response intensity	415.030(183)	0.062	0.969	8144	8689

Note: Maximum likelihood results. All results represent standardized solutions.

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TABLE 4

Weak and strong invariance models for Surgency/Extraversion.

Models	X^2 (*df*)	RMSEA	CFI	AIC	BIC
Full weak invariance	19.479 (11)	0.048	0.99	7744	8091
Full strong invariance	51.014 (18)	0.074	0.97	7761	8076

Note: Maximum likelihood results. All results represent standardized solutions.

TABLE 5

Summary of ANOVAs & h^2 analyses

ANOVA Model	*N*	Mean	SEM	*p*-value	h^2
Sire grouping (Overall)					
Orientation/Regulation	144	0.431	0.035	**0.015**	**0.17**
Negative affectivity	144	0.015	0.050	**0.001**	**0.18**
Surgency/extraversion	144	0.590	0.028	**0.007**	**0.17**
Dam grouping (Overall)					
Orientation/Regulation	270	0.374	0.026	**<0.0001**	**0.17**
Negative affectivity	270	−0.072	0.037	0.556	0.12
Surgency/Extraversion	270	0.595	0.019	0.531	0.12
Sire grouping (NR only)					
Orientation/Regulation	96	0.477	0.042	**0.047**	**0.17**
Negative affectivity	96	−0.162	0.059	**0.001**	**0.19**
Surgency/Extraversion	96	0.537	0.036	**0.018**	**0.18**
Dam Grouping (NR only)					
Orientation/Regulation	127	0.514	0.038	0.059	0.16
Negative affectivity	127	−0.213	0.051	0.675	0.11
Surgency/Extraversion	127	0.590	0.030	0.834	0.10
Sire Grouping (MR only)					
Orientation/Regulation	50	0.335	0.056	0.077	0.17
Negative Affectivity	50	0.219	0.099	0.829	0.07
Surgency/Extraversion	50	0.618	0.046	**0.035**	0.**19**
Dam Grouping (MR only)					
Orientation/Regulation	38	0.303	0.056	**0.017**	**0.19**
Negative affectivity	38	0.159	0.106	0.722	0.09
Surgency/Extraversion	38	0.500	0.046	0.109	0.17

Bold values are significant at $p < 0.05$.