Interindividual differences in neonatal sociality and emotionality predict juvenile social status in rhesus monkeys

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Research Highlights

- We examined whether neonatal sociality, temperament, and early social experience predicted juvenile social status in rhesus macaques (*Macaca mulatta*).
- Greater neonatal imitation and emotional reactivity, measured in the first month of life, predicted higher juvenile social status 2-3 years later.
- Infants with normative early social experiences (presence of the mother and social group) achieved higher juvenile status than infants reared with peers only.
- Neonatal characteristics and early social experience may have stable, long-term effects on the development of social status.

Abstract

In humans, socioeconomic status (SES) has profound outcomes on socio-emotional development and health. However, while much is known about the *consequences* of SES, little research has examined the *predictors* of SES due to the longitudinal nature of such studies. We sought to explore whether interindividual differences in neonatal sociality, temperament, and early social experiences predicted juvenile social status in rhesus monkeys (*Macaca mulatta*), as a proxy for SES in humans. We performed neonatal imitation tests in infants' first week of life and emotional reactivity assessments at 2 and 4 weeks of age. We examined whether these traits, as well the rearing environment in the first 8 months of life (with the mother or with same-aged peers only) and maternal social status predicted juvenile (2-3 years old) social status following the formation of peer social groups at 8 months. We found that infants who exhibited higher rates of neonatal imitation and newborn emotional reactivity achieved higher social status as juveniles, as did infants who were reared with their mothers, compared to infants reared with peers. Maternal social status was only associated with juvenile status for infant dyads reared in the same maternal group, indicating that relative social relationships were transferred through social experience. These results suggest that neonatal imitation and emotional reactivity may reflect ingrained predispositions towards sociality that predict later outcomes, and that non-normative social experiences can alter socio-developmental trajectories. Our results indicate that neonatal characteristics and early social experiences predict later social outcomes in adolescence, including gradients of social stratification.

Keywords: mother-rearing, dominance rank, early life adversity, social behavior, social hierarchy, nonhuman primate

Introduction

While there is no consensus on the definition of socioeconomic status (SES), it generally refers to an individual's relative social standing and access to various resources (i.e., capital, education, income, healthcare, social integration). Unsurprisingly, therefore, there is a considerable amount of research examining the relationship between SES and developmental outcomes such as emotion regulation, cognitive functioning, stress, and overall health across the lifespan (e.g., Bradley & Corwyn, 2002; Farah, 2017; Sapolsky, 2004). For example, in humans, individuals with low, compared to high, SES generally have poorer emotion regulation and higher rates of mood disorders (Hackman, Farah, & Meaney, 2010; South & Krueger, 2011), score lower on cognitive functioning tests (Lyu & Burr, 2016), have decreased cortical surface area (Noble et al., 2015), and exhibit higher levels of stress (Dettenborn, Tietze, Bruckner, & Kirschbaum, 2010; Rippe et al., 2016) resulting in poor cardiac outcomes (Marmot, Rose, & Hamilton, 1978) and greater mortality (Marmot, 2004; Marmot et al., 1991; Marmot, Shipley, & Rose, 1984). Thus, the effect of SES on other outcomes is clear.

However, while much research has focused on the developmental *consequences* of SES, little research has examined the developmental *predictors* that have the potential to influence SES. This gap in the field is largely due to the longitudinal nature of such studies and the potential heritability of SES (Deckers, Falk, Kosse, & Schildberg-Hörisch, 2015). Indeed, there are two non-mutually exclusive theories: social causation theory and social selection theory (Hackman, Farah, & Meaney, 2010; Ortega & Corzine, 1990; Johnson, Cohen, Dohrenwend, Link, & Brook, 1999). 'Social causation theory' hypothesizes that SES may affect developmental outcomes, whereas 'social selection theory' theory hypothesizes that, from early in development, children's characteristics (e.g., emotional reactivity, sociality) or environment may predispose them to a particular SES. 'Social causation theory' addresses the *consequences* of SES, while 'social selection theory' assesses the *predictors* of SES. For the purposes of this study, we chose to specifically address 'social selection theory' and therefore examine the developmental predictors of SES.

One developmental characteristic potentially influencing developmental trajectories is neonatal imitation, a newborn's ability to match modeled behaviors shortly after birth, which has been reported in humans (Heimann, 1989; Heimann, Nelson, & Schaller, 1989; Meltzoff & Moore, 1977), chimpanzees (*Pan troglodytes*; Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2004), and rhesus macaques (*Macaca mulatta*; Ferrari et al., 2006). Neonatal imitation has been proposed as a possible intrinsic predisposition towards sociality (Heimann, Nelson, & Schaller, 1989; Suddendorf, Oostenbroek, Nielsen, & Slaughter, 2012) that may predict developmental outcomes (rhesus macaques: Ferrari et al., 2009). As such, human infants classified as neonatal imitators, compared to non-imitators, exhibit fewer gaze aversions during a face-to-face mother-infant interaction at 3 months of age (Heimann, 1989, 1998). However, the most extensive research regarding the developmental outcomes of neonatal imitation comes from experimental studies with rhesus macaques. Infant macaques classified as neonatal imitators look more at faces (Simpson, Paukner, Suomi, & Ferrari, 2014), especially the eyes, (Paukner, Simpson, Ferrari, Mrozek, & Suomi, 2014); exhibit better gaze following at 7 months of age (i.e., looking where another individual looks; Simpson, Miller, Ferrari, Suomi, & Paukner, 2016); engage in more frequent social interactions with peers and less anxious behaviors at one year of age (Kaburu, Paukner, Simpson, Suomi, & Ferrari, 2016); and exhibit increased affiliative behaviors compared to their non-imitative peers following oxytocin administration (Simpson et al., 2014). The extent to which neonatal imitation could predict later social status remains unclear, and longitudinal studies are particularly important for understanding whether neonatal imitation may indeed reflect an early marker of infant sociability.

Another potential predictor of SES is temperament, defined as individual differences in emotional, motor, and attentional reactivity (Rothbart & Derryberry, 1981), which can be reliably measured in human newborns and is stable by 2-4 years of age (Lemery, Goldsmith, Klinnert, & Mrazek, 1999; Pedlow, Sanson, Prior, & Oberklaid, 1993). Individual differences in toddler temperament (i.e., 24 months of age), such as negative emotional reactivity (e.g., intensity and duration of affective arousal; distress: Rothbart & Derryberry, 1981), have been described as contributing to various social outcomes, such as increased conflict with peers during toddlerhood (Calkins, Gill, Johnson, & Smith, 1999). Increased conflict with others may be deleterious for other social outcomes as well. Accordingly, low self-control of emotions as early as 3 years of age has been associated with higher unemployment in early adulthood (i.e., 15-21 years) and higher adult criminal behavior (Caspi, 2000). Children exhibiting greater negative emotionality later in childhood (8 years of age) also had lower educational attainment and long-term unemployment as adults (27-36 years: Kokko, Pulkkinen, & Puustinen, 2000; Kokko, Bergman, & Pulkkinen, 2003). Together, these studies suggest that emotional reactivity may be a stable attribute of an individual that can predict important life outcomes years later (Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007). It is less clear, however, whether neonatal temperament (i.e., in the first month of life) can predict later outcomes beyond infancy (Nagy, 2011).

Finally, early social experiences also remain a critical influence on developmental trajectories, including later social status. For example, in humans, individuals without a stable caregiver and who experience physical abuse have increased risks for homelessness (Herman, Susser, Struening, & Link, 1997), and infant rhesus macaques reared in the absence of the mother (i.e., without a stable caregiver) also have lower social status in juvenility and adulthood likely due to improper attachment tendencies (Bastian, Sponberg, Suomi, & Higley, 2003) and dysregulation of the hypothalamic-pituitary-adrenocortical (HPA) axis (Dettmer et al., 2016). Moreover, the SES that an individual is "born into" may create a social and financial vacuum thereby limiting (or promoting) opportunities (e.g., nutrition, education, healthcare), which may have prognostic effects on the development of SES. Conversely, traits related to SES may be heritable. Similar to their mothers, children from high SES families are more patient, more altruistic, score higher on IQ tests, and are less risk-seeking than children from low SES families (Deckers et al., 2015). These consequences of childhood SES may result in a positive feedback loop, whereby childhood SES may influence personality, which in turn, may influence subsequent SES. Similarly, in rhesus macaques, infants of high-status mothers also exhibit different temperamental traits compared to low-status monkeys, such as increased levels of activity, lowered startle responses, and reduced cortisol levels (Suarez-Jimenez et al., 2013) and exhibit different socio-visual preferences (i.e., looking more at the eyes, Paukner, Slonecker, Murphy, Wooddell, & Dettmer, 2017), potentially predisposing them to achieve higher status as adults as well. The social class that one is "born into" therefore may have future impacts on later social status due to similar genetic characteristics (inheritance of maternal temperament; e.g., see Sullivan, Mendoza, & Capitanio, 2011 in rhesus macaques) or environmental characteristics (e.g., social opportunities), which are difficult to tease apart in human studies. Studies in nonhuman primates offer a unique opportunity to test the influence of genetics and environment on later social status.

Like humans, rhesus monkeys exhibit large variations in emotionality (Capitanio, 2010), neonatal imitation (Simpson et al., 2014), and sociality (Capitanio, Hawkley, Cole, & Cacioppo, 2014; Feczko, Bliss-Moreau, Walum, Pruett, & Parr, 2016). Furthermore, social status in monkeys is often used as a proxy for SES in humans (e.g., Chiao, 2010; Dettmer et al., 2016; Hackman, Farah, & Meaney, 2010; Sapolsky, 2004; Willard & Shively, 2016) due to the asymmetries in power and access to resources among high and low status individuals. For example, high-ranking monkeys, much like humans, also reap the benefits of high social status; compared to low-ranking monkeys, they have lowered risks of predation (Ron, Henzi, & Motro, 1996), enjoy priority access to food resources (Deutsch & Lee, 1991), exhibit greater reproductive success and earlier reproductive debut (Rodriguez-Llanes, Verbeke, & Finlayson, 2009; Pittet, Johnson, & Hinde, 2017), experience increased levels of social support and affiliation (Snyder-Mackler et al., 2016), and have lowered risks of illness (Sapolsky, 2005) and chronic stress (Qin et al., 2013; Sapolsky, 2005), all of which may collectively increase the lifespan.

Social status also influences a number of behavioral attributes in rhesus monkeys (such as boldness and grooming frequencies; Kohn et al., 2016; Snyder-Mackler et al., 2016), which are amenable to change following changes in social status. In addition, the juvenile period is an especially lengthy period in primates during which a considerable amount of energy expenditure is invested in development (Altmann & Alberts, 2005; Leigh, 2004; Walker, Burger, Wagner, & von Rueden, 2006) and learning to navigate their complex social lives (Barale, Rubenstein, & Beehner, 2015; Joffe, 1997). These attributes therefore make juvenility an ideal period to investigate how neonatal characteristics and early social experience predict social status during a highly transitional developmental period.

Although there are many similarities between social status in rhesus macaques (e.g., dominance rank) and SES in humans, it is also imperative to note that there are important differences. Notably, social status in nonhuman primates reflects social asymmetries among individuals within a common group, whereas SES in humans reflects social asymmetries based on demographic attributes with individuals of different classes potentially being anonymous to one another (Kaplan & Manuck, 1999). This difference is meaningful because this indicates that social status within primate groups is dependent on group membership, which may change and consequently change social status (i.e., Tung et al., 2012; Snyder-Mackler et al., 2016), whereas SES in humans is theoretically independent of group membership and potentially stable. However, given that the group memberships remained stable throughout the study period and that the broad definition of SES in humans refers to the relative access to power with which they can obtain resources (McLoyd, 1998), we and others (e.g., Jarrell et al., 2008; Massart et al., 2017; Snyder-Mackler et al., 2018; Vandeleest et al., 2016) argue that the social construct of status in nonhuman primates is still a good translational model for humans.

In the current study, we sought to explore whether interindividual differences in newborns' sociality and temperament—neonatal imitation and emotional reactivity in the first month of life—as well as early social experiences (across the first 8 months of life) predict juvenile social status in rhesus monkeys. To address these questions, we performed neonatal imitation testing within the first week of life and a neurobehavioral assessment measuring emotional reactivity twice in the first month of life on infant rhesus macaques. The neonatal imitation task assessed the frequency with which infant macaques imitated facial gestures performed by a human caretaker. The emotional reactivity task measured components relating to irritability, consolability, and distress during neurobehavioral assessments. In addition, we also measured two components of early social experience for the first 8 months of life: the rearing environment (being reared with mothers within a larger social group, or peers only) and maternal social status. At 2-3 years of age, we studied the social hierarchy of 33 individuals to examine whether the neonatal characteristics and early social experience predicted later juvenile social status. Given that neonatal imitation has been hypothesized to be a precursor to advanced sociality and that macaque imitators initiate more social interactions and exhibit fewer anxious behaviors at one-year of age (Kaburu et al., 2016), we hypothesized that those who displayed greater frequencies of neonatal imitation in infancy, compared to less-imitative newborns, would achieve a higher social status as juveniles (*prediction 1*). We also predicted that infants who exhibited greater emotional reactivity (as opposed to being calm and passive), compared to those who were less reactive, would achieve a lower social status (*prediction 2*). Similar to previous studies (Bastian et al., 2003; Dettmer et al., 2016), we predicted that infants reared with their mothers (and then subsequently separated) would achieve higher social statuses in adolescence than infants reared solely with peers (*prediction 3*). Finally, rhesus macaques are a matrilineal social species and undergo a process called “maternal rank inheritance” (Kawai, 1958) by which offspring attain adjacent ranks to their mothers through maturation via vigorous matrilineal support in aggressive interactions (Berman, 1980; Wooddell, Kaburu, Suomi, & Dettmer, 2016; Wooddell, Kaburu, Murphy, Suomi, & Dettmer, 2017). We therefore predicted that if social status is a socially acquired process—i.e., through maternal social transmission (Berman, 1980)—then infants from high-ranking mothers would achieve higher statuses if they were mother-reared, but not if they were reared with peers only (*prediction 4*). Alternatively, if social status has a potential genetic component (Massart et al., 2017, Tung et al., 2012), maternal social status should predict juvenile social status regardless of previous social experience (i.e., rearing).

Materials and Methods

Subjects and rearing

Subjects were 33 rhesus monkeys (*Macaca mulatta*) born in two cohorts in 2013 (*N*=19) and 2014 (*N*=14). All infants were born and reared at the Laboratory of Comparative Ethology (LCE) at the National Institutes of Health (NIH) Animal Center in Poolesville, Maryland. All procedures described adhered to the NIH Guide for the Care and Use of Laboratory Animals (National Research Council, 2010; National Institutes of Health, 1985), the US Public Health Service's Policy on Humane Care and Use of Laboratory Animals, and were approved by the *Eunice Kennedy Shriver* National Institute of Child Health and Human Development Animal Care and Use Committee (ACUC). Infants were randomly assigned at birth to one of two rearing conditions, described below.

Mother-reared subjects

Thirteen (5 males; 8 females) mother-reared infants (9 from 2013 cohort; 4 from 2014 cohort) were born and reared in one of five harem groups consisting of 10-12 adult females, one adult male, and several similar-aged infants. No juveniles were present in these groups, and each mother only had a single offspring in the group. Given that there was only one adult male, infants born into the same harem group were paternal half-siblings. The groups lived in enclosures consisting of indoor (2.44 × 3.05 × 2.21 m) and outdoor (2.44 × 3.0 × 2.44 m) portions, equipped with perches, swings, barrels, and wood shavings. All infants had *ab libitum* access to Purina LabDiet #5045 High Protein Monkey Diet chow (St. Louis, MO). Fresh fruit and seeds were provided once daily. Mother-reared infants lived with their mothers and social group until approximately 8 months of age, after which they were placed into one large social group (along with non-mother-reared infants; described below) consisting of similar-aged peers and one adult male.

Non-mother-reared subjects

Twenty (9 males; 11 females) infants (10 from 2013 cohort; 10 from 2014 cohort) were born from mothers in the harem groups, but on the day of birth (typically by 8 am), infants were separated from their mothers and reared in a nursery for unrelated studies. All housing arrangements contained an inanimate fleece surrogate, loose pieces of fleece fabric, and various plush, plastic, and rubber toys. For the first month of life, infants could see and hear, but not physically contact, other infants of similar age. Human caretakers were present for 13 hours each day, and interacted with infants every two hours for feeding and cleaning in addition to other assessments. Infants were bottle fed Similac formula. Starting at 16 days of age, infants were additionally offered Purina LabDiet #5045 High Protein Monkey Diet chow. Lights were on from 7:00 to 21:00. For unrelated studies, infants were randomly assigned to one of two rearing conditions when the youngest infant of the group turned 37 days. Half of these infants (*N*=9: 3 males; 6 females) were surrogate-peer-reared, individually placed in a large cage and given daily two-hour play sessions with three to four other peers each weekday. The other half of these infants (*N*=11: 6 males, 5 females) were peer-reared, placed in a large cage with three to four peers, providing continuous access to other peers. Infants were individually housed in incubators (51 × 38 × 43 cm) for the first two weeks of life and in larger cages (61 × 61 × 76 cm) thereafter, until approximately 8 months of age, when all infants were introduced into a novel social group (along with mother-reared infants) of similar-aged peers and one adult male (described below). We classified all infants reared in the nursery as non-mother-reared (*N*=20) because sample sizes precluded us from analyzing peer-reared (*N*=11) and surrogate-peer-reared (*N*=9) infants separately.

Group formation

At approximately 8 months of age, all infants were moved into one large social group consisting of both mother-reared and non-mother-reared infants and one unrelated adult male. The groups lived in indoor (7.3 x 3.4 x 3.7m) and outdoor (corncrib measuring 5.03 x 5.03 x 5.49 m) habitats. The mother-reared and non-mother-reared subjects born in 2013 all lived in one social group, and the mother-reared and non-mother-reared subjects born in 2014 all lived in another, distinct social group. It is important to note that these social groups now consisted only of similar-aged peers plus one unrelated adult male; the mothers were not present and could not influence the social hierarchy of the peer groups.

Data collection

Neonatal imitation

We tested 19 of the 20 non-mother-reared infants for neonatal imitation three times per day, every other day, in the first week of life (days 1-2, 3-4, 5-6, and 7-8), for up to four days (Kaburu et al., 2016; Simpson et al., 2016). Neonatal imitation tests were done on non-mother-reared infants only due to the extensive nature of testing (although previous studies have been conducted on mother-reared infants; see Vanderwert et al., 2015). One infant was rejected from his mother and subsequently reared in the nursery and therefore was not included in neonatal imitation testing due to his older age (34 days) before arriving in the nursery. There was at least an hour between each test session. A demonstrator presented infants with three stimuli, one during each session, at a distance of approximately 30 cm at eye-level with the infant: a lipsmacking gesture (LPS; rapid opening and closing of the mouth), a tongue protrusion gesture (TP; slow protrusion and retraction of the tongue, ca. one gesture per second), and a nonsocial control condition (CTRL; a white plastic disk with orthogonal stripes—which were either black/red or green/yellow—slowly rotated clockwise and counter-clockwise). Each stimulus type was presented once a day to infants; the order of stimulus presentations remained the same for each infant but was randomized between infants. In each test session, one experimenter held the infant, a second experimenter—the demonstrator—served as the source of the stimuli, and a third experimenter was the time-keeper who ensured stimuli were presented for appropriate lengths. All sessions were videotaped. Individual demonstrators were randomly assigned to conditions but remained consistent across days within each infant.

At the beginning of a trial, there was a 40-s baseline phase in which the demonstrator displayed a calm, neutral facial expression (or the still disk in CTRL). During the subsequent stimulus phase, the demonstrator displayed a facial movement (LPS or TP) or rotated the disk for 20-s followed by a still/neutral facial expression (still disk in CTRL) period for 20-s. This movement-still face sequence was repeated once and ended with an additional 20-s movement period (total of 100-s stimulus phase). Facial gesture responses (LPS and TP) were coded by an experimenter blind to the experimental condition. For analyses, responses in each phase were converted to a rate by adjusting to a common time period.

We examined interindividual differences in neonatal imitation by utilizing a continuous behavioral measure of the strength of the imitative response (Simpson, Paukner, Sclafani, Suomi, & Ferrari, 2013). We computed two imitative indices (i.e., imitation strength scores), one for LPS and one for TP, using the averaged gesture rate across days, with the following formulas:

$$\text{LPS Imitation Index} = [(\text{LPS}_{\text{Stim}} - \text{LPS}_{\text{Base1}})_{\text{LPS cond}}] - [(\text{LPS}_{\text{Stim}} - \text{LPS}_{\text{Base1}})_{\text{CTRL cond}}]$$

$$\text{TP Imitation Index} = [(\text{TP}_{\text{Stim}} - \text{TP}_{\text{Base1}})_{\text{TP cond}}] - [(\text{TP}_{\text{Stim}} - \text{TP}_{\text{Base1}})_{\text{CTRL cond}}]$$

For LPS Imitation Index, we first calculated a difference score: LPS rate produced in Stimulus and subtracted from it LPS rate produced in Baseline. This difference score was computed for the LPS and CTRL conditions, and we subtracted the CTRL condition from the LPS condition to obtain the difference of the difference scores. The resulting value was positive, and thus infants are classified as imitators, if there was a greater imitative response in the LPS condition, and zero or negative (non-imitators) if there was an equal or greater response in the CTRL condition. We calculated the TP Imitation Index in the same way: rate of TP gestures produced in the Stimulus period and subtracted from it the TP rate produced in Baseline, and subtracted this difference score in the CTRL condition from the difference score in the TP condition.

Neurobehavioral assessments

At days 14 and 30 ± 2 days of life, we performed routine neonatal neurobehavioral assessments (the Brazelton Neonatal Behavioral Assessment Scale; Schneider, Moore, Suomi, & Champoux, 1991) on 31 of the 33 infants (12 mother-reared; 19 non-mother-reared). Two infants (1 mother-reared and 1 non-mother-reared) were excluded from neonatal assessments, as one infant was too old for testing before coming to the nursery, and one was only tested on day 14. The 30-min assessments examined infants' reflexes, motor development, and emotional reactivity. Infants were rated on each measure on a scale ranging from 0 to 2 in 0.5 increments, with 0 reflecting a very weak response and 2 reflecting a very strong response. Two variables (irritability and consolability) were originally scored during the assessment in reverse order (0 reflecting a very strong response and 2 reflecting a very weak response) and were thus reverse coded for consistency so that all variables were scored with higher values reflecting higher reactivity. We examined six emotional reactivity variables, which consisted of soothability, the infants' ability to calm itself; irritability/ consolability, the amount of struggle exhibited by the infant during the assessment; and the predominant state of the infant (calm or stressed; see also Suarez-Jimenez et al., 2013). All six variables were combined to create an 'emotional reactivity composite' variable for both days 14 and 30 of life. Emotional reactivity composite variables could therefore range from 0 (absent emotional reactivity) to 12 (very strong emotional reactivity). We examined both the average emotional reactivity composite (average for the first month of life) and the change in emotional reactivity (day 30 emotional reactivity composite - day 14 emotional reactivity composite).

Early social experience: rearing environment and maternal social status

Infants were pseudo-randomized to one of the two rearing conditions: mother-rearing or non-mother-rearing for the first 8 months of life. Briefly, infants were balanced across mothers to ensure that a mother had both mother-reared and non-mother-reared infants over time and were balanced across both high and low status mothers. For this study, observers were blind to the rearing condition of the subjects and obtained this information retrospectively from a longitudinal database following the establishment of the juvenile hierarchies. Mothers' social statuses were established via longitudinal data collection by multiple observers (inter-rater reliability ≥ 85%). Dominance data were collected in two, 30-min sessions per week in which all instances of aggression (threats, chases, attacks) and submission (displacements, fear grimaces) were recorded (see also Dettmer et al., 2016). Social status was calculated from these dominance interactions (n=2,417) via Elo-rating (Albers & de Vries, 2001; Neumann et al., 2011). We used the *elo.sequence* function (Neumann et al., 2011) in R software (v 3.4.0) to generate Elo-ratings, with the initial value set at 1,000 and the k value set at 200. We calculated an average Elo-rating for each infant's mother starting at the infants' birth (in either 2013 or 2014 depending on the cohort) through the first 8 months of life. As group sizes differed, we calculated the relative social status by taking the number of animals outranked by the target animal, divided this number by the total number of animals in the social group, and subtracted it from 1. Relative social status therefore ranged from 0.05 (lowest-ranking) to 1 (highest-ranking).

Juvenile social status

Social status on the two juvenile social groups was collected from March 2016 to end of May 2016, when the subjects were two (2014 cohort) and three years old (2013 cohort), representing the juvenile period. Dominance data were collected 2-3 times per week by one observer in which all instances of aggression (threats, chases, attacks) and submission (displacements, fear grimaces) were recorded, following the same scheme as the maternal harem group observations. 1,412 interactions were recorded for the 2013 cohort, and 959 interactions were recorded for the 2014 cohort. Social status was established via Elo-rating. We calculated an average Elo-rating for the entire study period and then transformed this average Elo-rating into a relative social status following the same procedure as for the mothers.

Statistical analyses

Linear regression was used to assess whether neonatal imitation in the first week of life and the emotional reactivity from days 14 to 30 of life predicted significant variation in relative juvenile social status within their social groups. Given that the sample sizes were different for each of these variables (neonatal imitation: n=19; emotional reactivity: n=31), we ran two separate linear regressions to maximize the sample size for each variable. To examine whether early social experience (rearing and maternal social status) predicted significant variation in juvenile relative social status, we ran a separate multiple linear regression (as rearing and maternal social status were available on all subjects; N=33), reporting the change in the R^2 value. All means are reported as mean ± SD. Unless indicated otherwise, all analyses were performed in SPSS 24. Alpha values were set at 0.05.

Results

Do neonatal imitation and emotional reactivity predict juvenile social status?

Neonatal imitation scores in the first week of life ranged from -6.60 to 13.88 (M=1.30 ± 5.10). Linear regression revealed that the imitation index positively predicted juvenile social status ($F(1,17)=5.38$, $R^2=0.24$, $P=0.03$, $\beta=0.49$; see Figure 1 and Table 1), with imitators achieving higher social statuses at 2-3 years of age than non-imitators (supporting *prediction 1*). It is important to note that neonatal imitation data only included non-mother-reared infants.

Emotional reactivity scores from the neurobehavioral assessments in the first month of life ranged from 0 to 12 on day 14 (M=4.55 ± 4.19) and day 30 (M=6.14 ± 4.48). The change from days 14 to 30 ranged from -2.5 to 6.5 (M=1.60 ± 2.38). Mother-reared infants exhibited greater average emotional reactivity composites for the first month of life than non-mother-reared infants ($F(1,29)= 83.09$, $R^2=0.74$, $P<0.001$, $\beta=0.86$), but there was no significant difference in the change with age (i.e., day 30- day 14) in emotional reactivity ($F(1,29)= 0.81$, $R^2=0.03$, $P=0.38$, $\beta=0.17$) across mother-reared and non-mother reared infants. We therefore only examined whether the change with age in emotional reactivity predicted juvenile social status, as rearing was a possible confounding variable. The change in emotional reactivity from days 14 to 30 of life positively predicted a significant portion of the variance in juvenile social status at 2-3 years old (F(1,29)= 5.50, R^2=0.16, P=0.03, β=0.40; see Figure 2), with infants exhibiting higher increases in emotional reactivity achieving subsequent higher social status (contradicting *prediction 2*). When analyzing mother-reared and non-mother-reared infants independently, the emotional reactivity change did not predict variance in juvenile social status (mother-reared: F(1,10)= 3.10, R^2=0.24, P=0.11, β=0.49; non-mother-reared: F(1,17)= 1.86, R^2=0.10, P=0.19, β=0.31). Also, when analyzing mother-reared and non-mother-reared infants independently, the average emotional reactivity composite across the first month of life did not predict juvenile social status (mother-reared: F(1,10)= 0.03, R^2=0.003, P=0.87, β=0.05; non-mother-reared: F(1,17)= 0.63, R^2=0.04, P=0.44, β=0.19). The imitation index and change in emotional reactivity were not collinear (V=1.0).

Does early social experience (rearing and maternal social status) predict juvenile social status?

Rearing and maternal social status were not significantly correlated (Pearson correlation: r=-0.19, P=0.28, N=33). Out of the two components measuring early social experience, only rearing significantly predicted variation in juvenile social status (rearing: ΔR^2=0.19, P=0.01, see Figure 3; supporting *prediction 3;* maternal social status: ΔR^2=0.009, P=0.57). When analyzing mother-reared and non-mother-reared subjects independently, maternal social status still did not predict variation in juvenile social status (mother-reared: F(1,11)=0.38, R^2=0.03, P=0.55, β=0.18; non-mother-reared: F(1,18)=0.02, R^2=0.001, P=0.90, β=0.03; failing to support *prediction 4*). However, not all mother-reared subjects were reared in the same harem groups in infancy (N=5 different groups), thus providing no social experience with the other mothers in the other rearing groups. This experience with the other mothers may be an important requisite for acquisition of relative status (Wooddell et al., 2017). When we examined mother-reared dyads that were reared together in infancy, 8/10 (80%) of their dyadic statuses were predicted by their mothers' dyadic statuses, which is greater than what could be expected by chance (one sample t test: $t_9=2.25$, $P=0.05$, $d=0.71$). This result suggests that maternal social status may not predict infants' status overall, but only relative status with those reared together in infancy.

Discussion

In this study, newborn macaques that displayed more frequent neonatal imitation attained higher social status as juveniles than their peers who exhibited less frequent imitative responses. Neonatal imitation may reflect ingrained predispositions for advanced social skills (Kaburu et al., 2016; Paukner et al., 2014; Simpson, Murray, Paukner, & Ferrari, 2014; Simpson et al., 2016). The finding that imitators attained higher social status suggests that these individuals may have advanced social competency in other regards (e.g., aggression, coalitions, play; Bissonnette et al., 2015; Borgeaud & Bshary, 2015), consistent with previous reports (Kaburu et al., 2016; Paukner et al., 2014; Simpson et al., 2016), at least up until one year of age. Our study extends these findings into juvenility and encompasses one of the most important social characteristics of rhesus monkeys: social status.

Unfortunately, we were unable to analyze neonatal imitation responses in mother-reared infants, which will be an important comparison to make with non-mother-reared infants, and is an exciting avenue for future studies. Mother-reared infants exhibit a greater neurological signature in response to lipsmacking imitation than non-mother-reared infants (Vanderwert et al., 2015), as many macaque mothers engage in frequent face-to-face affiliative interactions (Ferrari, Paukner, Ionica, & Suomi, 2009), which may potentially preprogram their infants to socially complex cues, setting them up for future social success (Dettmer et al., 2016; Simpson et al., 2014). Here, we also replicated previous work showing that mother-reared macaques attain higher social status than non-mother-reared infants (Bastian et al., 2003; Dettmer et al., 2016), suggesting an intriguing association between early maternal interactions (mutual gaze, lipsmacking, etc.), neonatal imitation, and future social status following maternal separation. Future research should investigate these potential relationships. Finally, it is worthy to note that the non-mother-reared infant macaques in this study were required to imitate a human and not a conspecific, which could potentially complicate the interpretation of our findings. However, a previous study found that neonatal macaques that engaged in greater lipsmacking imitation with a human observer also displayed heightened visual preferences with a conspecific avatar (i.e., a video of a computerized interactive monkey; Paukner et al., 2014), indicating that imitators display similar behavioral responses regardless of the model species (e.g., Kaburu et al., 2016; Paukner et al., 2014; Simpson et al., 2014; 2016).

Additionally, we found that infants who exhibited increases in negative affective reactivity from days 14 to 30 of life also subsequently attained higher social status as juveniles. The acquisition of high status in monkey society has ubiquitous consequences impacting nearly every facet of everyday life from food acquisition (Deutsch & Lee, 1991) to health (Sapolsky, 2005). The finding that the increase in negative emotional reactivity scores was related to the attainment of high social status highlights that emotional reactivity can have adaptive consequences. Conversely, previous studies with children, ranging from 3 to 8 years old, have found that greater negative emotional reactivity may be associated with lower SES, measured as educational attainment and unemployment (Caspi, 2000; Kokko, Bergman, & Pulkkinen, 2003; Kokko, Pulkkinen, & Puustinen, 2000), indicating potential maladaptive consequences of emotional reactivity. While we found the opposite in monkeys, there are a few possible explanations. The most parsimonious explanation for the different results is that they may be due to differences in the methodological techniques and definitions used to assess emotional reactivity in humans and monkeys, with parent or teacher reports of disruptive behavior being commonly utilized for children (Kokko, Bergman, & Pulkkinen, 2003; Kokko, Pulkkinen, & Puustinen, 2000), and behavioral reactions towards neurobehavioral testing (e.g., vocalizations, soothability, etc.) being utilized for monkeys (Schneider et al., 1991; Suarez-Jimenez et al., 2013). Another possibility is that the different results may be due to the differences in attainment of social status in human and monkey societies and the definitions of social status. Social status (e.g., dominance rank) in monkeys is achieved primarily via aggression (and other social mechanisms), whereas social status attainment in humans is multi-faceted and not fully understood and encompasses a variety of definitions (education, income, social hierarchies). This difference is important to note: emotional reactivity may have adaptive consequences for monkey society by influencing agonistic behavior and vigilance (thereby helping in the attainment of high social status), which may be less adaptive for human society (Bernstein & Gordon, 1974). However, it is also possible that the specific social status we measured in monkeys (i.e., the social hierarchy of same-aged peers) may be more equivalent to social hierarchies in human gangs of teenagers. In fact, overt aggression is an important predictor of status and popularity in humans during the late elementary and teen years (see Koski, Xie, & Olson, 2015 for a review). Our findings indicate that emotional reactivity therefore may have important implications for social status specifically in teenage groups with social hierarchies. Given that social status in humans can encompass a variety of definitions (education level, income, popularity, social hierarchy, etc.), it is also important to emphasize that monkey studies may be applicable to certain aspects of social status that are ecologically relevant to both species (i.e., social hierarchies are applicable to both monkeys and humans; education and income are not). Nevertheless, nonhuman primates serve as a valuable model in the behavioral and physiological mechanisms shaping social status (Chiao, 2010).

Our study augments previous findings in humans that temperament can relate to important life outcomes years later, such as SES (Kokko, Bergman, & Pulkkinen, 2003; Kokko, Pulkkinen, & Puustinen, 2000; Roberts et al., 2007), and we have extended these predictors to encompass nonhuman primates even earlier in infancy and to include neonatal temperament. Our findings indicate that while the neonatal period includes rapid development and emergence of systems, some aspects of neonatal sociality (e.g., neonatal imitation) and temperament (e.g., emotional reactivity) may be stable and reliable predictors over the course of maturation (also reported in human neonates until at least 2 years: Bornstein et al., 2015; Matheny, Riese, & Wilson, 1985; Riese, 1987; Tirosh, Hard, Abadi, Berger, & Cohen, 1992; Worobey & Blajda, 1989).

In addition, previous monkey studies found a causal relationship between social status and personality (Kohn et al., 2016; Snyder-Mackler et al., 2016), whereby social status, and changes therein, affected personality, indicating that the social environment can shape personality. Here, we found that temperament measured early in life predicted social status years later. Fairbanks et al. (2004) found that adolescent (3 to 4 years of age) male vervet monkeys (*Chlorocebus pygerythrus*) that were rated as more impulsive were more likely to become alpha males as adults (6 years of age) compared to those that were less impulsive. However, as adults the alpha males decreased in impulsivity to similar levels as low-ranking males, suggesting a possible moderation of current status on personality. Ideally, we would have concurrent measures of juvenile temperament to examine the stability of neonatal characteristics and the relationship between current social status and temperament. In the future, we plan to analyze a variety of socio-cognitive assessments through developmental stages to examine the stability of temperament over time and effects on social, cognitive, and health outcomes. Unsurprisingly, previous research found that temperament measured in infant rhesus macaques (at 3 months of age) is relatively stable across a variety of socio-cognitive tasks up to at least 4.5 years of age (Capitanio, 1999) and can predict other forms of sociality such as affiliation (Weinstein & Capitanio, 2008).

In accordance with previous findings (Bastian et al., 2003; Dettmer et al., 2016), we found that infants reared with their mothers achieved higher social status than infants reared solely with peers. As Bastian et al. (2003) hypothesized, the lack of species-typical social environments in early development may alter socio-developmental trajectories, resulting in subsequently lower social status. The long-lasting consequences of early socially impoverished environments or early life adversity (such as institutionalization) are evident in humans: children with early life adversity, compared to those without adversity, are more likely to attempt suicide in later life (Dube et al., 2001), exhibit blunted stress responses to psychosocial stressors (McLaughlin et al., 2015), have atypically large amygdalas (Tottenham et al., 2009) resulting in difficulty in understanding emotional facial expressions (Wismer Fries & Pollak, 2004) and emotional regulation (Tottenham et al., 2009), and develop fewer close relationships with peers (Hodges & Tizard, 1989) or conversely exhibit indiscriminate sociality (for a review see Zeanah, 2000). The presence of consistent primary caretakers (e.g., mother, father, grandparents) early in life, who serve as valuable attachment figures (Tarullo & Gunnar, 2005), enable infants to learn to recognize important social cues and how to respond appropriately, which is a fundamental aspect of sociality (Kanai et al., 2012). Indeed, adult non-mother-reared monkeys, compared to mother-reared monkeys, display greater behavioral inhibition in response to a mild challenge (an unfamiliar human; Corcoran et al., 2012). A greater tendency for inhibition may explain why non-mother-reared monkeys, as compared to mother-reared monkeys, were more likely to become socially subordinate, as they may be more likely to respond to conspecific social cues with submission (freezing or moving away) rather than aggression.

We found little evidence supporting the notion that macaque social status is inherent or that infants are born into a particular social stratum, independent of experience. The absence of the mother (and other kin), and the resulting lack of a similar status in the infants as in the mothers in the current study, indicates that maternal rank inheritance is achieved via the mother's presence, at least during some point in development. The mother does not need to be present indefinitely, but likely needs to be present to "jumpstart" the process of rank inheritance. Indeed, non-mother-reared monkeys, who have not experienced their mother's social status, did not achieve a similar status as their mothers. The same null finding for mother-reared animals at first is counterintuitive to this argument. However, it is important to note that, even for mother-reared infants, there were many (5) harem groups, meaning that some groups of infants were not reared together for the first 8 months. Mother-reared infants that were reared together however, did obtain identical relative statuses to each other as their mothers, 2-3 years later, meaning the offspring of the higher-ranking mother was also higher-ranking than the peers with whom they were reared. Our results provide preliminary evidence that maternal rank inheritance persists for mother-reared individuals initially reared together. This finding is similar to previous studies indicating that infants reared in large multigenerational groups obtained identical relative ranks as their mothers following separation (Wooddell et al., 2017), even following social instability, suggesting that their relative ranks were socially transmitted early in development (i.e., within the first 8 months of life) and persistent. Given that social status is a characteristic of relationships, it is possible that early relationships in infancy may be maintained through at least juvenility. While considerably less is known about the social transmission of SES in human societies, which are understandably more complex than monkey societies, future research should investigate potential genetic and prenatal/postnatal environmental sources of SES transmission (Huston, McLoyd, & Coll, 1997).

This study is not without limitations. First, our small sample size warrants future investigation and replication. In addition, while the change in emotional reactivity from days 14 to 30 of life was not predicted by rearing, the average emotionality score across both ages was, revealing that as a whole, mother-reared infants were overall more emotionally reactive than non-mother-reared infants. This result is likely not only due to rearing itself, but also possibly unfamiliarity with the testing environment (see Wachs, Pollitt, Cueto, & Jacoby, 2004 for findings in human neonates in laboratory compared to home environments) and being temporarily separated from the mother (which in itself can cause distress). In the future, neurobehavioral assessments should assess reactivity in the mother's presence (Muschinski et al., 2016; Parr et al., 2016; Vanderwert et al., 2015) or using novel apparatuses where mother-reared infants can voluntarily partake in cognitive studies (Dettmer, Murphy, & Suomi, 2015). This adjustment will allow for a meaningful comparison between different rearing environments without the possible confound of distress from maternal separation for mother-reared individuals. Finally, although our study was intentionally designed to examine predictors of status acquisition in groups in which there were no sources of kin support that would undoubtedly influence status outcomes, we acknowledge that in naturalistic groups (including humans), the absence of kin support would be unlikely. In groups where there is a social transmission of status (such as in rhesus macaques), it may be more likely that individual characteristics may instead influence other properties of status acquisition, such as the speed. For example, male white-faced capuchins (*Cebus capucinus*) that are more extraverted attained alpha status sooner than less extraverted males (Perry, Godoy, Lammers, & Lin, 2017), indicating that personality can affect the speed of status acquisition in wild settings.

Social status is a pervasive factor in the social lives of many primates, including humans, with an understanding of others' status beginning in early development (Gazes, Hampton, & Lourenco, 2015; Mascaro & Csibra, 2012; Pun, Birch, & Baron, 2016; Pun, Birch, & Baron, 2017), underscoring the ecological relevance of social asymmetries. Given the profound consequences of social status on development, nonhuman primates are an important translational model for SES in humans. The present study has begun to lay the groundwork for future studies taking a multi-tiered approach to investigate links between interindividual differences and SES across the lifespan.

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Table Legends

Table 1: Summary of results for predictors of juvenile social status in peer groups of rhesus monkeys.

Figure Legends

Figure 1: Infants that engaged in higher frequencies of neonatal imitation in the first week of life attained higher juvenile social statuses than infants who engaged in less frequent neonatal imitation.

Figure 2: Infants that had higher increases in negative emotional reactivity during neurobehavioral assessments between days 14 and 30 of life attained higher social statuses as juveniles than infants who exhibited lower increases in reactivity.

Figure 3: Mother-reared infants had higher social statuses as juveniles than infants that were reared with peers only.

Table 1.
Predictors of social status in peer groups of juvenile rhesus monkeys

Predictor (outcome: juvenile social status)	Sample size	Mean ± SD	R^2 value, β, P value
Neonatal Imitation (days 1-7 of life)	19	1.30 ± 5.10	0.24, 0.49, P=0.03
Emotional Reactivity (day 14 of life)	31	4.55±4.19	N/A
Emotional Reactivity (day 30 of life)	31	6.14±4.48	N/A
Emotional Reactivity Composite (first month of life), Non-mother-reared only	19	2.54±2.47	0.04, 0.19, P=0.44
Emotional Reactivity Composite (first month of life), Mother-reared only	12	9.79±1.51	0.003, 0.05, P=0.87
Change in Emotional Reactivity (day 30-day 14 of life)	31	1.60±2.38	0.16, 0.40, P=0.03
Change in Emotional Reactivity, (day 30-day 14 of life) Non-mother-reared only	19	1.29 ± 2.59	0.10, 0.31, P=0.19
Change in Emotional Reactivity, (day 30-day 14 of life) Mother-reared only	12	2.08 ± 2.02	0.24, 0.49, P=0.11
Rearing (first 8-months of life)	33	N/A	Δ=0.19, P=0.01
Maternal Social Status	33	0.57±0.31	Δ=0.009, P=0.57
Maternal Social Status, Non-mother-reared only	20	0.62±0.28	0.001, 0.03, P=0.90
Maternal Social Status, Mother-reared only	13	0.50±0.36	0.03, 0.18, P=0.55

Figure 1.

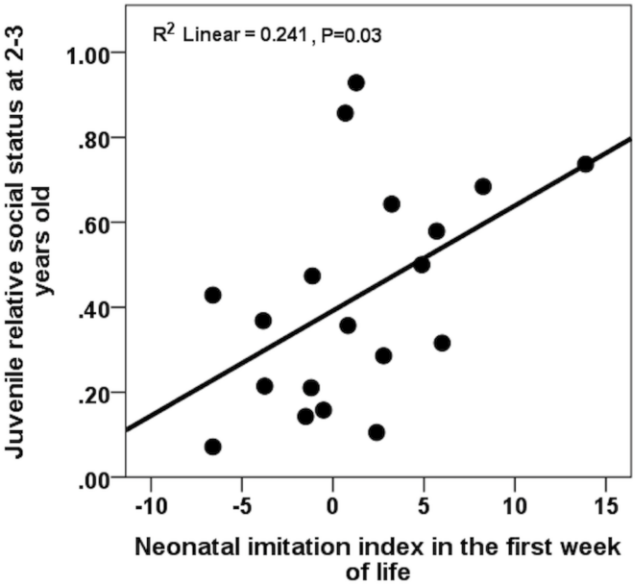
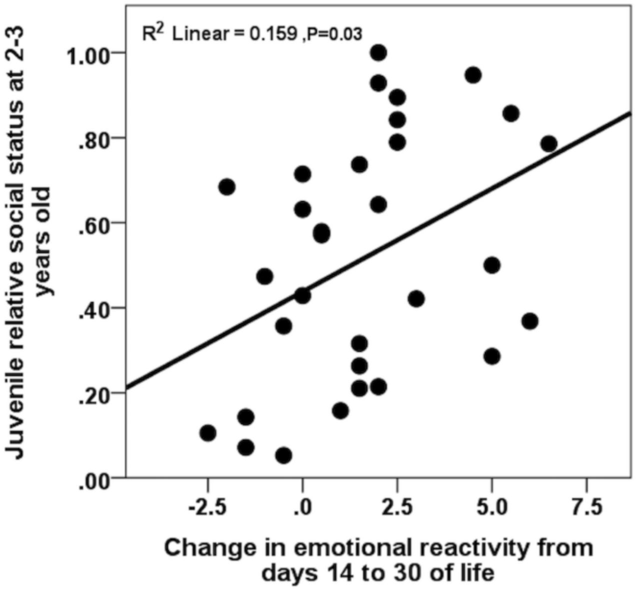
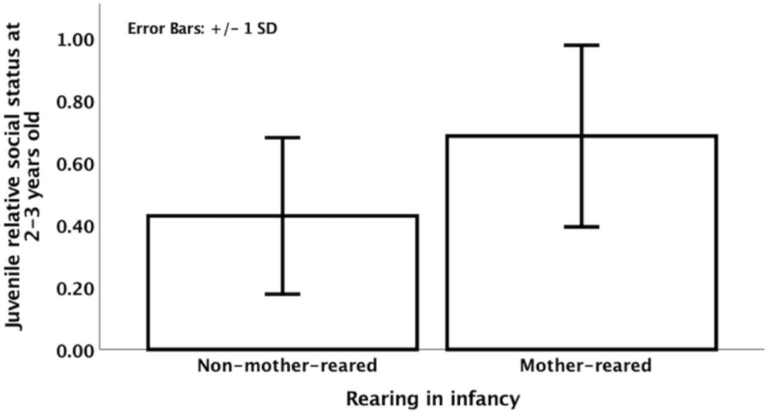

R^2 Linear = 0.241, P=0.03
Juvenile relative social status at 2-3 years old
1.00
.80
.60
.40
.20
.00
-10
-5
0
5
10
15
Neonatal imitation index in the first week of life

Figure 2.


R^2 Linear = 0.159 ,P=0.03
Juvenile relative social status at 2-3 years old
1.00
.80
.60
.40
.20
.00
-2.5
.0
2.5
5.0
7.5
Change in emotional reactivity from days 14 to 30 of life

956 Figure 3.



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