

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

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24 **Research Highlights**

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

33 **Abstract**

34 In humans, socioeconomic status (SES) has profound outcomes on socio-emotional
35 development and health. However, while much is known about the *consequences* of SES, little
36 research has examined the *predictors* of SES due to the longitudinal nature of such studies. We
37 sought to explore whether interindividual differences in neonatal sociality, temperament, and
38 early social experiences predicted juvenile social status in rhesus monkeys (*Macaca mulatta*), as
39 a proxy for SES in humans. We performed neonatal imitation tests in infants' first week of life
40 and emotional reactivity assessments at 2 and 4 weeks of age. We examined whether these traits,
41 as well the rearing environment in the first 8 months of life (with the mother or with same-aged
42 peers only) and maternal social status predicted juvenile (2-3 years old) social status following
43 the formation of peer social groups at 8 months. We found that infants who exhibited higher
44 rates of neonatal imitation and newborn emotional reactivity achieved higher social status as
45 juveniles, as did infants who were reared with their mothers, compared to infants reared with
46 peers. Maternal social status was only associated with juvenile status for infant dyads reared in

47 the same maternal group, indicating that relative social relationships were transferred through
48 social experience. These results suggest that neonatal imitation and emotional reactivity may
49 reflect ingrained predispositions towards sociality that predict later outcomes, and that non-
50 normative social experiences can alter socio-developmental trajectories. Our results indicate that
51 neonatal characteristics and early social experiences predict later social outcomes in adolescence,
52 including gradients of social stratification.

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

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67 **Introduction**

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

81 However, while much research has focused on the developmental *consequences* of SES,
82 little research has examined the developmental *predictors* that have the potential to influence
83 SES. This gap in the field is largely due to the longitudinal nature of such studies and the
84 potential heritability of SES (Deckers, Falk, Kosse, & Schildberg-Hörisch, 2015). Indeed, there
85 are two non-mutually exclusive theories: social causation theory and social selection theory
86 (Hackman, Farah, & Meaney, 2010; Ortega & Corzine, 1990; Johnson, Cohen, Dohrenwend,
87 Link, & Brook, 1999). 'Social causation theory' hypothesizes that SES may affect
88 developmental outcomes, whereas 'social selection theory' theory hypothesizes that, from early
89 in development, children's characteristics (e.g., emotional reactivity, sociality) or environment

90 may predispose them to a particular SES. ‘Social causation theory’ addresses the *consequences*
91 of SES, while ‘social selection theory’ assesses the *predictors* of SES. For the purposes of this
92 study, we chose to specifically address ‘social selection theory’ and therefore examine the
93 developmental predictors of SES.

94 One developmental characteristic potentially influencing developmental trajectories is
95 neonatal imitation, a newborn’s ability to match modeled behaviors shortly after birth, which has
96 been reported in humans (Heimann, 1989; Heimann, Nelson, & Schaller, 1989; Meltzoff &
97 Moore, 1977), chimpanzees (*Pan troglodytes*; Myowa-Yamakoshi, Tomonaga, Tanaka, &
98 Matsuzawa, 2004), and rhesus macaques (*Macaca mulatta*; Ferrari et al., 2006). Neonatal
99 imitation has been proposed as a possible intrinsic predisposition towards sociality (Heimann,
100 Nelson, & Schaller, 1989; Suddendorf, Oostenbroek, Nielsen, & Slaughter, 2012) that may
101 predict developmental outcomes (rhesus macaques: Ferrari et al., 2009). As such, human infants
102 classified as neonatal imitators, compared to non-imitators, exhibit fewer gaze aversions during a
103 face-to-face mother-infant interaction at 3 months of age (Heimann, 1989, 1998). However, the
104 most extensive research regarding the developmental outcomes of neonatal imitation comes from
105 experimental studies with rhesus macaques. Infant macaques classified as neonatal imitators look
106 more at faces (Simpson, Paukner, Suomi, & Ferrari, 2014), especially the eyes, (Paukner,
107 Simpson, Ferrari, Mrozek, & Suomi, 2014); exhibit better gaze following at 7 months of age
108 (i.e., looking where another individual looks; Simpson, Miller, Ferrari, Suomi, & Paukner,
109 2016); engage in more frequent social interactions with peers and less anxious behaviors at one
110 year of age (Kaburu, Paukner, Simpson, Suomi, & Ferrari, 2016); and exhibit increased
111 affiliative behaviors compared to their non-imitative peers following oxytocin administration
112 (Simpson et al., 2014). The extent to which neonatal imitation could predict later social status

113 remains unclear, and longitudinal studies are particularly important for understanding whether
114 neonatal imitation may indeed reflect an early marker of infant sociability.

115 Another potential predictor of SES is temperament, defined as individual differences in
116 emotional, motor, and attentional reactivity (Rothbart & Derryberry, 1981), which can be
117 reliably measured in human newborns and is stable by 2-4 years of age (Lemery, Goldsmith,
118 Klinnert, & Mrazek, 1999; Pedlow, Sanson, Prior, & Oberklaid, 1993). Individual differences in
119 toddler temperament (i.e., 24 months of age), such as negative emotional reactivity (e.g.,
120 intensity and duration of affective arousal; distress: Rothbart & Derryberry, 1981), have been
121 described as contributing to various social outcomes, such as increased conflict with peers during
122 toddlerhood (Calkins, Gill, Johnson, & Smith, 1999). Increased conflict with others may be
123 deleterious for other social outcomes as well. Accordingly, low self-control of emotions as early
124 as 3 years of age has been associated with higher unemployment in early adulthood (i.e., 15-21
125 years) and higher adult criminal behavior (Caspi, 2000). Children exhibiting greater negative
126 emotionality later in childhood (8 years of age) also had lower educational attainment and long-
127 term unemployment as adults (27-36 years: Kokko, Pulkkinen, & Puustinen, 2000; Kokko,
128 Bergman, & Pulkkinen, 2003). Together, these studies suggest that emotional reactivity may be a
129 stable attribute of an individual that can predict important life outcomes years later (Roberts,
130 Kuncel, Shiner, Caspi, & Goldberg, 2007). It is less clear, however, whether neonatal
131 temperament (i.e., in the first month of life) can predict later outcomes beyond infancy (Nagy,
132 2011).

133 Finally, early social experiences also remain a critical influence on developmental
134 trajectories, including later social status. For example, in humans, individuals without a stable
135 caregiver and who experience physical abuse have increased risks for homelessness (Herman,

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

158 Like humans, rhesus monkeys exhibit large variations in emotionality (Capitanio, 2010),
159 neonatal imitation (Simpson et al., 2014), and sociality (Capitanio, Hawkley, Cole, & Cacioppo,
160 2014; Feczko, Bliss-Moreau, Walum, Pruett, & Parr, 2016). Furthermore, social status in
161 monkeys is often used as a proxy for SES in humans (e.g., Chiao, 2010; Dettmer et al., 2016;
162 Hackman, Farah, & Meaney, 2010; Sapolsky, 2004; Willard & Shively, 2016) due to the
163 asymmetries in power and access to resources among high and low status individuals. For
164 example, high-ranking monkeys, much like humans, also reap the benefits of high social status;
165 compared to low-ranking monkeys, they have lowered risks of predation (Ron, Henzi, & Motro,
166 1996), enjoy priority access to food resources (Deutsch & Lee, 1991), exhibit greater
167 reproductive success and earlier reproductive debut (Rodriguez-Llanes, Verbeke, & Finlayson,
168 2009; Pittet, Johnson, & Hinde, 2017), experience increased levels of social support and
169 affiliation (Snyder-Mackler et al., 2016), and have lowered risks of illness (Sapolsky, 2005) and
170 chronic stress (Qin et al., 2013; Sapolsky, 2005), all of which may collectively increase the
171 lifespan.

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

181 Although there are many similarities between social status in rhesus macaques (e.g.,
182 dominance rank) and SES in humans, it is also imperative to note that there are important
183 differences. Notably, social status in nonhuman primates reflects social asymmetries among
184 individuals within a common group, whereas SES in humans reflects social asymmetries based
185 on demographic attributes with individuals of different classes potentially being anonymous to
186 one another (Kaplan & Manuck, 1999). This difference is meaningful because this indicates that
187 social status within primate groups is dependent on group membership, which may change and
188 consequently change social status (i.e., Tung et al., 2012; Snyder-Mackler et al., 2016), whereas
189 SES in humans is theoretically independent of group membership and potentially stable.
190 However, given that the group memberships remained stable throughout the study period and
191 that the broad definition of SES in humans refers to the relative access to power with which they
192 can obtain resources (McLoyd, 1998), we and others (e.g., Jarrell et al., 2008; Massart et al.,
193 2017; Snyder-Mackler et al., 2018; Vandeleest et al., 2016) argue that the social construct of
194 status in nonhuman primates is still a good translational model for humans.

195 In the current study, we sought to explore whether interindividual differences in
196 newborns' sociality and temperament—neonatal imitation and emotional reactivity in the first
197 month of life—as well as early social experiences (across the first 8 months of life) predict
198 juvenile social status in rhesus monkeys. To address these questions, we performed neonatal
199 imitation testing within the first week of life and a neurobehavioral assessment measuring
200 emotional reactivity twice in the first month of life on infant rhesus macaques. The neonatal
201 imitation task assessed the frequency with which infant macaques imitated facial gestures
202 performed by a human caretaker. The emotional reactivity task measured components relating to
203 irritability, consolability, and distress during neurobehavioral assessments. In addition, we also

204 measured two components of early social experience for the first 8 months of life: the rearing
205 environment (being reared with mothers within a larger social group, or peers only) and maternal
206 social status. At 2-3 years of age, we studied the social hierarchy of 33 individuals to examine
207 whether the neonatal characteristics and early social experience predicted later juvenile social
208 status. Given that neonatal imitation has been hypothesized to be a precursor to advanced
209 sociality and that macaque imitators initiate more social interactions and exhibit fewer anxious
210 behaviors at one-year of age (Kaburu et al., 2016), we hypothesized that those who displayed
211 greater frequencies of neonatal imitation in infancy, compared to less-imitative newborns, would
212 achieve a higher social status as juveniles (*prediction 1*). We also predicted that infants who
213 exhibited greater emotional reactivity (as opposed to being calm and passive), compared to those
214 who were less reactive, would achieve a lower social status (*prediction 2*). Similar to previous
215 studies (Bastian et al., 2003; Dettmer et al., 2016), we predicted that infants reared with their
216 mothers (and then subsequently separated) would achieve higher social statuses in adolescence
217 than infants reared solely with peers (*prediction 3*). Finally, rhesus macaques are a matrilineal
218 social species and undergo a process called “maternal rank inheritance” (Kawai, 1958) by which
219 offspring attain adjacent ranks to their mothers through maturation via vigorous matrilineal
220 support in aggressive interactions (Berman, 1980; Wooddell, Kaburu, Suomi, & Dettmer, 2016;
221 Wooddell, Kaburu, Murphy, Suomi, & Dettmer, 2017). We therefore predicted that if social
222 status is a socially acquired process—i.e., through maternal social transmission (Berman,
223 1980)—then infants from high-ranking mothers would achieve higher statuses if they were
224 mother-reared, but not if they were reared with peers only (*prediction 4*). Alternatively, if social
225 status has a potential genetic component (Massart et al., 2017, Tung et al., 2012), maternal social
226 status should predict juvenile social status regardless of previous social experience (i.e., rearing).

227 **Materials and Methods**

228 *Subjects and rearing*

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

238 *Mother-reared subjects*

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

249 group (along with non-mother-reared infants; described below) consisting of similar-aged peers
250 and one adult male.

251 *Non-mother-reared subjects*

252 Twenty (9 males; 11 females) infants (10 from 2013 cohort; 10 from 2014 cohort) were
253 born from mothers in the harem groups, but on the day of birth (typically by 8 am), infants were
254 separated from their mothers and reared in a nursery for unrelated studies. All housing
255 arrangements contained an inanimate fleece surrogate, loose pieces of fleece fabric, and various
256 plush, plastic, and rubber toys. For the first month of life, infants could see and hear, but not
257 physically contact, other infants of similar age. Human caretakers were present for 13 hours each
258 day, and interacted with infants every two hours for feeding and cleaning in addition to other
259 assessments. Infants were bottle fed Similac formula. Starting at 16 days of age, infants were
260 additionally offered Purina LabDiet #5045 High Protein Monkey Diet chow. Lights were on
261 from 7:00 to 21:00. For unrelated studies, infants were randomly assigned to one of two rearing
262 conditions when the youngest infant of the group turned 37 days. Half of these infants ($N=9$: 3
263 males; 6 females) were surrogate-peer-reared, individually placed in a large cage and given daily
264 two-hour play sessions with three to four other peers each weekday. The other half of these
265 infants ($N=11$: 6 males, 5 females) were peer-reared, placed in a large cage with three to four
266 peers, providing continuous access to other peers. Infants were individually housed in incubators
267 ($51 \times 38 \times 43$ cm) for the first two weeks of life and in larger cages ($61 \times 61 \times 76$ cm) thereafter,
268 until approximately 8 months of age, when all infants were introduced into a novel social group
269 (along with mother-reared infants) of similar-aged peers and one adult male (described below).
270 We classified all infants reared in the nursery as non-mother-reared ($N=20$) because sample sizes

271 precluded us from analyzing peer-reared ($N=11$) and surrogate-peer-reared ($N=9$) infants
272 separately.

273 *Group formation*

274 At approximately 8 months of age, all infants were moved into one large social group
275 consisting of both mother-reared and non-mother-reared infants and one unrelated adult male.
276 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
277 m) habitats. The mother-reared and non-mother-reared subjects born in 2013 all lived in one
278 social group, and the mother-reared and non-mother-reared subjects born in 2014 all lived in
279 another, distinct social group. It is important to note that these social groups now consisted only
280 of similar-aged peers plus one unrelated adult male; the mothers were not present and could not
281 influence the social hierarchy of the peer groups.

282 *Data collection*

283 *Neonatal imitation*

284 We tested 19 of the 20 non-mother-reared infants for neonatal imitation three times per
285 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
286 (Kaburu et al., 2016; Simpson et al., 2016). Neonatal imitation tests were done on non-mother-
287 reared infants only due to the extensive nature of testing (although previous studies have been
288 conducted on mother-reared infants; see Vanderwert et al., 2015). One infant was rejected from
289 his mother and subsequently reared in the nursery and therefore was not included in neonatal
290 imitation testing due to his older age (34 days) before arriving in the nursery. There was at least
291 an hour between each test session. A demonstrator presented infants with three stimuli, one
292 during each session, at a distance of approximately 30 cm at eye-level with the infant: a

293 lipsmacking gesture (LPS; rapid opening and closing of the mouth), a tongue protrusion gesture
294 (TP; slow protrusion and retraction of the tongue, ca. one gesture per second), and a nonsocial
295 control condition (CTRL; a white plastic disk with orthogonal stripes—which were either
296 black/red or green/yellow—slowly rotated clockwise and counter-clockwise). Each stimulus type
297 was presented once a day to infants; the order of stimulus presentations remained the same for
298 each infant but was randomized between infants. In each test session, one experimenter held the
299 infant, a second experimenter—the demonstrator—served as the source of the stimuli, and a third
300 experimenter was the time-keeper who ensured stimuli were presented for appropriate lengths.
301 All sessions were videotaped. Individual demonstrators were randomly assigned to conditions
302 but remained consistent across days within each infant.

303 At the beginning of a trial, there was a 40-s baseline phase in which the demonstrator
304 displayed a calm, neutral facial expression (or the still disk in CTRL). During the subsequent
305 stimulus phase, the demonstrator displayed a facial movement (LPS or TP) or rotated the disk for
306 20-s followed by a still/neutral facial expression (still disk in CTRL) period for 20-s. This
307 movement-still face sequence was repeated once and ended with an additional 20-s movement
308 period (total of 100-s stimulus phase). Facial gesture responses (LPS and TP) were coded by an
309 experimenter blind to the experimental condition. For analyses, responses in each phase were
310 converted to a rate by adjusting to a common time period.

311 We examined interindividual differences in neonatal imitation by utilizing a continuous
312 behavioral measure of the strength of the imitative response (Simpson, Paukner, Sclafani, Suomi,
313 & Ferrari, 2013). We computed two imitative indices (i.e., imitation strength scores), one for
314 LPS and one for TP, using the averaged gesture rate across days, with the following formulas:
315

$$316 \quad \text{LPS Imitation Index} = [(LPS_{\text{Stim}} - LPS_{\text{Base1}})_{\text{LPS cond}}] - [(LPS_{\text{Stim}} - LPS_{\text{Base1}})_{\text{CTRL cond}}]$$

$$317 \quad \text{TP Imitation Index} = [(TP_{\text{Stim}} - TP_{\text{Base1}})_{\text{TP cond}}] - [(TP_{\text{Stim}} - TP_{\text{Base1}})_{\text{CTRL cond}}]$$

318

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

328 *Neurobehavioral assessments*

329 At days 14 and 30 ± 2 days of life, we performed routine neonatal neurobehavioral
 330 assessments (the Brazelton Neonatal Behavioral Assessment Scale; Schneider, Moore, Suomi, &
 331 Champoux, 1991) on 31 of the 33 infants (12 mother-reared; 19 non-mother-reared). Two infants
 332 (1 mother-reared and 1 non-mother-reared) were excluded from neonatal assessments, as one
 333 infant was too old for testing before coming to the nursery, and one was only tested on day 14.
 334 The 30-min assessments examined infants' reflexes, motor development, and emotional
 335 reactivity. Infants were rated on each measure on a scale ranging from 0 to 2 in 0.5 increments,
 336 with 0 reflecting a very weak response and 2 reflecting a very strong response. Two variables
 337 (irritability and consolability) were originally scored during the assessment in reverse order (0
 338 reflecting a very strong response and 2 reflecting a very weak response) and were thus reverse

339 coded for consistency so that all variables were scored with higher values reflecting higher
340 reactivity. We examined six emotional reactivity variables, which consisted of soothability, the
341 infants' ability to calm itself; irritability/ consolability, the amount of struggle exhibited by the
342 infant during the assessment; and the predominant state of the infant (calm or stressed; see also
343 Suarez-Jimenez et al., 2013). All six variables were combined to create an 'emotional reactivity
344 composite' variable for both days 14 and 30 of life. Emotional reactivity composite variables
345 could therefore range from 0 (absent emotional reactivity) to 12 (very strong emotional
346 reactivity). We examined both the average emotional reactivity composite (average for the first
347 month of life) and the change in emotional reactivity (day 30 emotional reactivity composite -
348 day 14 emotional reactivity composite).

349 *Early social experience: rearing environment and maternal social status*

350 Infants were pseudo-randomized to one of the two rearing conditions: mother-rearing or
351 non-mother-rearing for the first 8 months of life. Briefly, infants were balanced across mothers to
352 ensure that a mother had both mother-reared and non-mother-reared infants over time and were
353 balanced across both high and low status mothers. For this study, observers were blind to the
354 rearing condition of the subjects and obtained this information retrospectively from a
355 longitudinal database following the establishment of the juvenile hierarchies. Mothers' social
356 statuses were established via longitudinal data collection by multiple observers (inter-rater
357 reliability $\geq 85\%$). Dominance data were collected in two, 30-min sessions per week in which all
358 instances of aggression (threats, chases, attacks) and submission (displacements, fear grimaces)
359 were recorded (see also Dettmer et al., 2016). Social status was calculated from these dominance
360 interactions (n=2,417) via Elo-rating (Albers & de Vries, 2001; Neumann et al., 2011). We used
361 the *elo.sequence* function (Neumann et al., 2011) in R software (v 3.4.0) to generate Elo-ratings,

362 with the initial value set at 1,000 and the k value set at 200. We calculated an average Elo-rating
363 for each infant's mother starting at the infants' birth (in either 2013 or 2014 depending on the
364 cohort) through the first 8 months of life. As group sizes differed, we calculated the relative
365 social status by taking the number of animals outranked by the target animal, divided this
366 number by the total number of animals in the social group, and subtracted it from 1. Relative
367 social status therefore ranged from 0.05 (lowest-ranking) to 1 (highest-ranking).

368 *Juvenile social status*

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

378 *Statistical analyses*

379 Linear regression was used to assess whether neonatal imitation in the first week of life
380 and the emotional reactivity from days 14 to 30 of life predicted significant variation in relative
381 juvenile social status within their social groups. Given that the sample sizes were different for
382 each of these variables (neonatal imitation: n=19; emotional reactivity: n=31), we ran two
383 separate linear regressions to maximize the sample size for each variable. To examine whether

384 early social experience (rearing and maternal social status) predicted significant variation in
385 juvenile relative social status, we ran a separate multiple linear regression (as rearing and
386 maternal social status were available on all subjects; N=33), reporting the change in the R^2 value.
387 All means are reported as mean \pm SD. Unless indicated otherwise, all analyses were performed
388 in SPSS 24. Alpha values were set at 0.05.

389 **Results**

390 *Do neonatal imitation and emotional reactivity predict juvenile social status?*

391 Neonatal imitation scores in the first week of life ranged from -6.60 to 13.88 (M=1.30 \pm
392 5.10). Linear regression revealed that the imitation index positively predicted juvenile social
393 status (F(1,17)=5.38, R^2 =0.24, P=0.03, β =0.49; see Figure 1 and Table 1), with imitators
394 achieving higher social statuses at 2-3 years of age than non-imitators (supporting *prediction 1*).
395 It is important to note that neonatal imitation data only included non-mother-reared infants.

396 Emotional reactivity scores from the neurobehavioral assessments in the first month of
397 life ranged from 0 to 12 on day 14 (M=4.55 \pm 4.19) and day 30 (M=6.14 \pm 4.48). The change
398 from days 14 to 30 ranged from -2.5 to 6.5 (M=1.60 \pm 2.38). Mother-reared infants exhibited
399 greater average emotional reactivity composites for the first month of life than non-mother-
400 reared infants (F(1,29)= 83.09, R^2 =0.74, P<0.001, β =0.86), but there was no significant
401 difference in the change with age (i.e., day 30- day 14) in emotional reactivity (F(1,29)= 0.81,
402 R^2 =0.03, P=0.38, β =0.17) across mother-reared and non-mother reared infants. We therefore
403 only examined whether the change with age in emotional reactivity predicted juvenile social
404 status, as rearing was a possible confounding variable. The change in emotional reactivity from
405 days 14 to 30 of life positively predicted a significant portion of the variance in juvenile social

406 status at 2-3 years old ($F(1,29)= 5.50$, $R^2=0.16$, $P=0.03$, $\beta=0.40$; see Figure 2), with infants
 407 exhibiting higher increases in emotional reactivity achieving subsequent higher social status
 408 (contradicting *prediction 2*). When analyzing mother-reared and non-mother-reared infants
 409 independently, the emotional reactivity change did not predict variance in juvenile social status
 410 (mother-reared: $F(1,10)= 3.10$, $R^2=0.24$, $P=0.11$, $\beta=0.49$; non-mother-reared: $F(1,17)= 1.86$,
 411 $R^2=0.10$, $P=0.19$, $\beta=0.31$). Also, when analyzing mother-reared and non-mother-reared infants
 412 independently, the average emotional reactivity composite across the first month of life did not
 413 predict juvenile social status (mother-reared: $F(1,10)= 0.03$, $R^2=0.003$, $P=0.87$, $\beta=0.05$; non-
 414 mother-reared: $F(1,17)= 0.63$, $R^2=0.04$, $P=0.44$, $\beta=0.19$). The imitation index and change in
 415 emotional reactivity were not collinear ($V=1.0$).

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

417 Rearing and maternal social status were not significantly correlated (Pearson correlation:
 418 $r=-0.19$, $P=0.28$, $N=33$). Out of the two components measuring early social experience, only
 419 rearing significantly predicted variation in juvenile social status (rearing: $\Delta R^2=0.19$, $P=0.01$, see
 420 Figure 3; supporting *prediction 3*; maternal social status: $\Delta R^2=0.009$, $P=0.57$). When analyzing
 421 mother-reared and non-mother-reared subjects independently, maternal social status still did not
 422 predict variation in juvenile social status (mother-reared: $F(1,11)=0.38$, $R^2=0.03$, $P=0.55$,
 423 $\beta=0.18$; non-mother-reared: $F(1,18)=0.02$, $R^2=0.001$, $P=0.90$, $\beta=0.03$; failing to support
 424 *prediction 4*). However, not all mother-reared subjects were reared in the same harem groups in
 425 infancy ($N=5$ different groups), thus providing no social experience with the other mothers in the
 426 other rearing groups. This experience with the other mothers may be an important requisite for
 427 acquisition of relative status (Wooddell et al., 2017). When we examined mother-reared dyads
 428 that were reared together in infancy, 8/10 (80%) of their dyadic statuses were predicted by their

429 mothers' dyadic statuses, which is greater than what could be expected by chance (one sample t
430 test: $t_9=2.25$, $P=0.05$, $d=0.71$). This result suggests that maternal social status may not predict
431 infants' status overall, but only relative status with those reared together in infancy.

432 **Discussion**

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

443 Unfortunately, we were unable to analyze neonatal imitation responses in mother-reared
444 infants, which will be an important comparison to make with non-mother-reared infants, and is
445 an exciting avenue for future studies. Mother-reared infants exhibit a greater neurological
446 signature in response to lipsmacking imitation than non-mother-reared infants (Vanderwert et al.,
447 2015), as many macaque mothers engage in frequent face-to-face affiliative interactions (Ferrari,
448 Paukner, Ionica, & Suomi, 2009), which may potentially preprogram their infants to socially
449 complex cues, setting them up for future social success (Dettmer et al., 2016; Simpson et al.,
450 2014). Here, we also replicated previous work showing that mother-reared macaques attain
451 higher social status than non-mother-reared infants (Bastian et al., 2003; Dettmer et al., 2016),

452 suggesting an intriguing association between early maternal interactions (mutual gaze,
453 lipsmacking, etc.), neonatal imitation, and future social status following maternal separation.
454 Future research should investigate these potential relationships. Finally, it is worthy to note that
455 the non-mother-reared infant macaques in this study were required to imitate a human and not a
456 conspecific, which could potentially complicate the interpretation of our findings. However, a
457 previous study found that neonatal macaques that engaged in greater lipsmacking imitation with
458 a human observer also displayed heightened visual preferences with a conspecific avatar (i.e., a
459 video of a computerized interactive monkey; Paukner et al., 2014), indicating that imitators
460 display similar behavioral responses regardless of the model species (e.g., Kaburu et al., 2016;
461 Paukner et al., 2014; Simpson et al., 2014; 2016).

462 Additionally, we found that infants who exhibited increases in negative affective
463 reactivity from days 14 to 30 of life also subsequently attained higher social status as juveniles.
464 The acquisition of high status in monkey society has ubiquitous consequences impacting nearly
465 every facet of everyday life from food acquisition (Deutsch & Lee, 1991) to health (Sapolsky,
466 2005). The finding that the increase in negative emotional reactivity scores was related to the
467 attainment of high social status highlights that emotional reactivity can have adaptive
468 consequences. Conversely, previous studies with children, ranging from 3 to 8 years old, have
469 found that greater negative emotional reactivity may be associated with lower SES, measured as
470 educational attainment and unemployment (Caspi, 2000; Kokko, Bergman, & Pulkkinen, 2003;
471 Kokko, Pulkkinen, & Puustinen, 2000), indicating potential maladaptive consequences of
472 emotional reactivity. While we found the opposite in monkeys, there are a few possible
473 explanations. The most parsimonious explanation for the different results is that they may be due
474 to differences in the methodological techniques and definitions used to assess emotional

475 reactivity in humans and monkeys, with parent or teacher reports of disruptive behavior being
476 commonly utilized for children (Kokko, Bergman, & Pulkkinen, 2003; Kokko, Pulkkinen, &
477 Puustinen, 2000), and behavioral reactions towards neurobehavioral testing (e.g., vocalizations,
478 soothability, etc.) being utilized for monkeys (Schneider et al., 1991; Suarez-Jimenez et al.,
479 2013). Another possibility is that the different results may be due to the differences in attainment
480 of social status in human and monkey societies and the definitions of social status. Social status
481 (e.g., dominance rank) in monkeys is achieved primarily via aggression (and other social
482 mechanisms), whereas social status attainment in humans is multi-faceted and not fully
483 understood and encompasses a variety of definitions (education, income, social hierarchies). This
484 difference is important to note: emotional reactivity may have adaptive consequences for
485 monkey society by influencing agonistic behavior and vigilance (thereby helping in the
486 attainment of high social status), which may be less adaptive for human society (Bernstein &
487 Gordon, 1974). However, it is also possible that the specific social status we measured in
488 monkeys (i.e., the social hierarchy of same-aged peers) may be more equivalent to social
489 hierarchies in human gangs of teenagers. In fact, overt aggression is an important predictor of
490 status and popularity in humans during the late elementary and teen years (see Koski, Xie, &
491 Olson, 2015 for a review). Our findings indicate that emotional reactivity therefore may have
492 important implications for social status specifically in teenage groups with social hierarchies.
493 Given that social status in humans can encompass a variety of definitions (education level,
494 income, popularity, social hierarchy, etc.), it is also important to emphasize that monkey studies
495 may be applicable to certain aspects of social status that are ecologically relevant to both species
496 (i.e., social hierarchies are applicable to both monkeys and humans; education and income are

497 not). Nevertheless, nonhuman primates serve as a valuable model in the behavioral and
498 physiological mechanisms shaping social status (Chiao, 2010).

499 Our study augments previous findings in humans that temperament can relate to
500 important life outcomes years later, such as SES (Kokko, Bergman, & Pulkkinen, 2003; Kokko,
501 Pulkkinen, & Puustinen, 2000; Roberts et al., 2007), and we have extended these predictors to
502 encompass nonhuman primates even earlier in infancy and to include neonatal temperament. Our
503 findings indicate that while the neonatal period includes rapid development and emergence of
504 systems, some aspects of neonatal sociality (e.g., neonatal imitation) and temperament (e.g.,
505 emotional reactivity) may be stable and reliable predictors over the course of maturation (also
506 reported in human neonates until at least 2 years: Bornstein et al., 2015; Matheny, Riese, &
507 Wilson, 1985; Riese, 1987; Tirosh, Hard, Abadi, Berger, & Cohen, 1992; Worobey & Blajda,
508 1989).

509 In addition, previous monkey studies found a causal relationship between social status
510 and personality (Kohn et al., 2016; Snyder-Mackler et al., 2016), whereby social status, and
511 changes therein, affected personality, indicating that the social environment can shape
512 personality. Here, we found that temperament measured early in life predicted social status years
513 later. Fairbanks et al. (2004) found that adolescent (3 to 4 years of age) male vervet monkeys
514 (*Chlorocebus pygerythrus*) that were rated as more impulsive were more likely to become alpha
515 males as adults (6 years of age) compared to those that were less impulsive. However, as adults
516 the alpha males decreased in impulsivity to similar levels as low-ranking males, suggesting a
517 possible moderation of current status on personality. Ideally, we would have concurrent
518 measures of juvenile temperament to examine the stability of neonatal characteristics and the
519 relationship between current social status and temperament. In the future, we plan to analyze a

520 variety of socio-cognitive assessments through developmental stages to examine the stability of
521 temperament over time and effects on social, cognitive, and health outcomes. Unsurprisingly,
522 previous research found that temperament measured in infant rhesus macaques (at 3 months of
523 age) is relatively stable across a variety of socio-cognitive tasks up to at least 4.5 years of age
524 (Capitanio, 1999) and can predict other forms of sociality such as affiliation (Weinstein &
525 Capitanio, 2008).

526 In accordance with previous findings (Bastian et al., 2003; Dettmer et al., 2016), we
527 found that infants reared with their mothers achieved higher social status than infants reared
528 solely with peers. As Bastian et al. (2003) hypothesized, the lack of species-typical social
529 environments in early development may alter socio-developmental trajectories, resulting in
530 subsequently lower social status. The long-lasting consequences of early socially impoverished
531 environments or early life adversity (such as institutionalization) are evident in humans: children
532 with early life adversity, compared to those without adversity, are more likely to attempt suicide
533 in later life (Dube et al., 2001), exhibit blunted stress responses to psychosocial stressors
534 (McLaughlin et al., 2015), have atypically large amygdalas (Tottenham et al., 2009) resulting in
535 difficulty in understanding emotional facial expressions (Wisner Fries & Pollak, 2004) and
536 emotional regulation (Tottenham et al., 2009), and develop fewer close relationships with peers
537 (Hodges & Tizard, 1989) or conversely exhibit indiscriminate sociality (for a review see Zeanah,
538 2000). The presence of consistent primary caretakers (e.g., mother, father, grandparents) early in
539 life, who serve as valuable attachment figures (Tarullo & Gunnar, 2005), enable infants to learn
540 to recognize important social cues and how to respond appropriately, which is a fundamental
541 aspect of sociality (Kanai et al., 2012). Indeed, adult non-mother-reared monkeys, compared to
542 mother-reared monkeys, display greater behavioral inhibition in response to a mild challenge (an

543 unfamiliar human; Corcoran et al., 2012). A greater tendency for inhibition may explain why
544 non-mother-reared monkeys, as compared to mother-reared monkeys, were more likely to
545 become socially subordinate, as they may be more likely to respond to conspecific social cues
546 with submission (freezing or moving away) rather than aggression.

547 We found little evidence supporting the notion that macaque social status is inherent or
548 that infants are born into a particular social stratum, independent of experience. The absence of
549 the mother (and other kin), and the resulting lack of a similar status in the infants as in the
550 mothers in the current study, indicates that maternal rank inheritance is achieved via the mother's
551 presence, at least during some point in development. The mother does not need to be present
552 indefinitely, but likely needs to be present to "jumpstart" the process of rank inheritance. Indeed,
553 non-mother-reared monkeys, who have not experienced their mother's social status, did not
554 achieve a similar status as their mothers. The same null finding for mother-reared animals at first
555 is counterintuitive to this argument. However, it is important to note that, even for mother-reared
556 infants, there were many (5) harem groups, meaning that some groups of infants were not reared
557 together for the first 8 months. Mother-reared infants that were reared together however, did
558 obtain identical relative statuses to each other as their mothers, 2-3 years later, meaning the
559 offspring of the higher-ranking mother was also higher-ranking than the peers with whom they
560 were reared. Our results provide preliminary evidence that maternal rank inheritance persists for
561 mother-reared individuals initially reared together. This finding is similar to previous studies
562 indicating that infants reared in large multigenerational groups obtained identical relative ranks
563 as their mothers following separation (Wooddell et al., 2017), even following social instability,
564 suggesting that their relative ranks were socially transmitted early in development (i.e., within
565 the first 8 months of life) and persistent. Given that social status is a characteristic of

566 relationships, it is possible that early relationships in infancy may be maintained through at least
567 juvenility. While considerably less is known about the social transmission of SES in human
568 societies, which are understandably more complex than monkey societies, future research should
569 investigate potential genetic and prenatal/postnatal environmental sources of SES transmission
570 (Huston, McLoyd, & Coll, 1997).

571 This study is not without limitations. First, our small sample size warrants future
572 investigation and replication. In addition, while the change in emotional reactivity from days 14
573 to 30 of life was not predicted by rearing, the average emotionality score across both ages was,
574 revealing that as a whole, mother-reared infants were overall more emotionally reactive than
575 non-mother-reared infants. This result is likely not only due to rearing itself, but also possibly
576 unfamiliarity with the testing environment (see Wachs, Pollitt, Cueto, & Jacoby, 2004 for
577 findings in human neonates in laboratory compared to home environments) and being
578 temporarily separated from the mother (which in itself can cause distress). In the future,
579 neurobehavioral assessments should assess reactivity in the mother's presence (Muschinski et al.,
580 2016; Parr et al., 2016; Vanderwert et al., 2015) or using novel apparatuses where mother-reared
581 infants can voluntarily partake in cognitive studies (Dettmer, Murphy, & Suomi, 2015). This
582 adjustment will allow for a meaningful comparison between different rearing environments
583 without the possible confound of distress from maternal separation for mother-reared individuals.
584 Finally, although our study was intentionally designed to examine predictors of status acquisition
585 in groups in which there were no sources of kin support that would undoubtedly influence status
586 outcomes, we acknowledge that in naturalistic groups (including humans), the absence of kin
587 support would be unlikely. In groups where there is a social transmission of status (such as in
588 rhesus macaques), it may be more likely that individual characteristics may instead influence

589 other properties of status acquisition, such as the speed. For example, male white-faced
590 capuchins (*Cebus capucinus*) that are more extraverted attained alpha status sooner than less
591 extraverted males (Perry, Godoy, Lammers, & Lin, 2017), indicating that personality can affect
592 the speed of status acquisition in wild settings.

593 Social status is a pervasive factor in the social lives of many primates, including humans,
594 with an understanding of others' status beginning in early development (Gazes, Hampton, &
595 Lourenco, 2015; Mascaro & Csibra, 2012; Pun, Birch, & Baron, 2016; Pun, Birch, & Baron,
596 2017), underscoring the ecological relevance of social asymmetries. Given the profound
597 consequences of social status on development, nonhuman primates are an important translational
598 model for SES in humans. The present study has begun to lay the groundwork for future studies
599 taking a multi-tiered approach to investigate links between interindividual differences and SES
600 across the lifespan.

601

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933 **Table Legends**

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

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938 **Figure Legends**

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

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

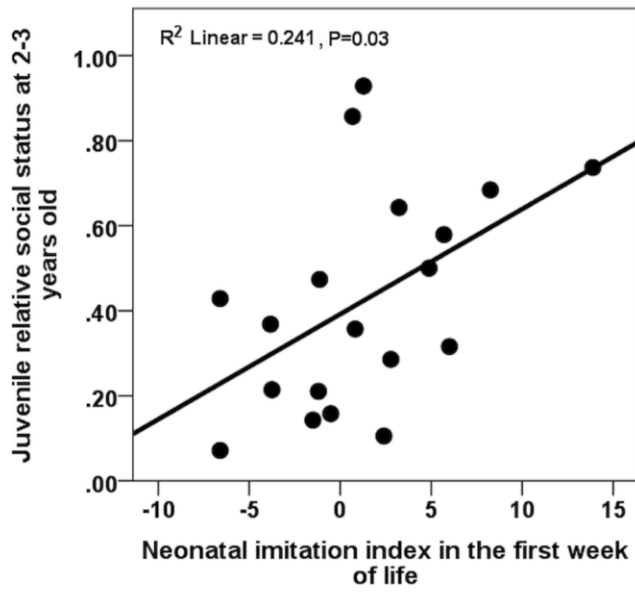
945 **Figure 3:** Mother-reared infants had higher social statuses as juveniles than infants that were
946 reared with peers only.

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

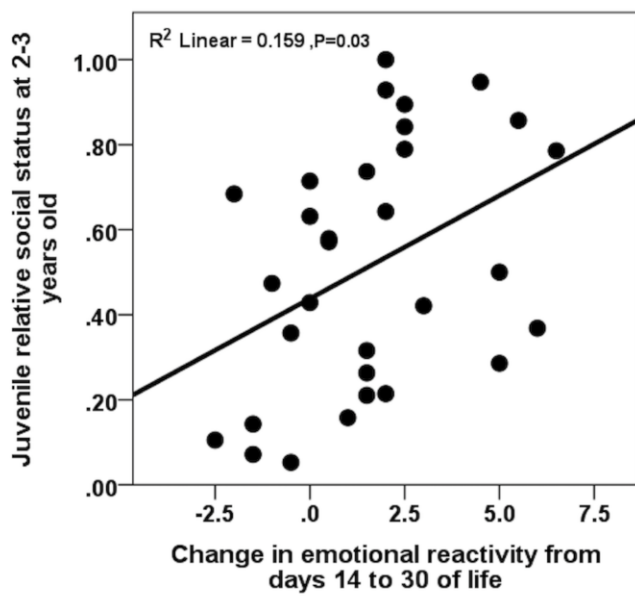
Predictor (outcome: juvenile social status)	Sample size	Mean \pm SD	R ² value, β , P value
Neonatal Imitation (days 1-7 of life)	19	1.30 \pm 5.10	0.24, 0.49, P=0.03
Emotional Reactivity (day 14 of life)	31	4.55 \pm 4.19	N/A
Emotional Reactivity (day 30 of life)	31	6.14 \pm 4.48	N/A
Emotional Reactivity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

950 Figure 1.

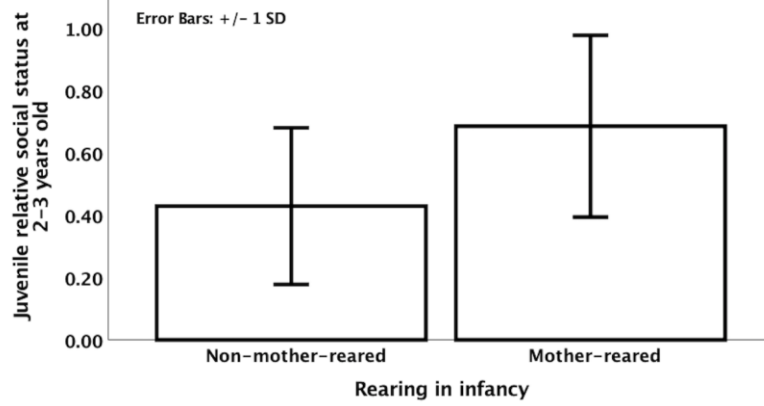


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953 Figure 2.

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956 Figure 3.



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