

1 Human and monkey infant attention to dynamic social and nonsocial stimuli  
2 Running title: Human and monkey infant attention

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28

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### Abstract

The present study explored behavioral norms for infant social attention in typically developing human and nonhuman primate infants. We examined the normative development of attention to dynamic social and nonsocial stimuli longitudinally in macaques (*Macaca mulatta*) at 1, 3, and 5 months of age ( $N=75$ ) and humans at 2, 4, 6, 8, and 13 months of age ( $N=69$ ) using eye tracking. All infants viewed concurrently played silent videos—one social video and one nonsocial video. Both macaque and human infants were faster to look to the social than the nonsocial stimulus, and both species grew faster to orient to the social stimulus with age. Further, macaque infants' social attention increased linearly from 1 to 5 months. In contrast, human infants displayed a non-linear pattern of social interest, with initially greater attention to the social stimulus, followed by a period of greater interest in the nonsocial stimulus, and then a rise in social interest from 6 to 13 months. Overall, human infants looked longer than macaque infants, suggesting humans have more sustained attention in the first year of life. These findings highlight potential species similarities and differences, and reflect a first step in establishing baseline patterns of early social attention development.

**Key terms:** nonhuman primate, sociality, infancy, comparative psychology, gaze

47 Human and nonhuman primate (NHP) infants preferentially attend to and process social  
48 stimuli—voices, bodies, biological motion, touch—compared to nonsocial stimuli (Gerson et al.,  
49 2016; Grossman, 2015; Shultz, Klin, & Jones, 2018). For example, human and NHP newborns  
50 orient more towards faces and face-shaped patterns compared to other images (Bard et al., 1992;  
51 Kuwahata, Adachi, Fujita, Tomonaga, & Matsuzawa, 2004; Paukner, Bower, Simpson, & Suomi,  
52 2013; Simpson, Jakobsen, Damon, Suomi, Ferrari, & Paukner, 2017; Valenza, Simion, Cassia, &  
53 Umiltà, 1996). These social preferences persist as infants develop (Sifre et al., 2018), while also  
54 becoming specialized for familiar categories, such as primary caretakers' species, race, and  
55 gender (Scott & Fava, 2013; Quinn, Lee, & Pascalis, 2019). These social sensitivities appear  
56 evolutionarily conserved across primates and emerge early in development, shaped by infants'  
57 social experiences (Simpson et al., 2019a). Yet, not all infants are equally socially attentive.

58 Individual differences in early social attention have important implications for  
59 development, with higher levels of social attention generally predicting more advanced social  
60 development. In humans, social attention in infancy is positively associated with later attachment  
61 security (Peltola, Forssman, Puura, van IJzendoorn, & Leppänen, 2015), joint attention  
62 (Schietecatte, Roeyers, & Warreyn, 2012), gaze following (Imafuku, Kawai, Niwa, Shinya,  
63 Inagawa, & Myowa-Yamakoshi, 2017), theory of mind (Wellman, Phillips, Dunphy-Lelii, &  
64 LaLonde, 2004; Yamaguchi, Kuhlmeier, Wynn, & VanMarle, 2009), and language development  
65 (Tenenbaum, Sobel, Sheinkopf, Malle, & Morgan, 2015) in toddlers and preschoolers. These  
66 individual differences in social attention appear early. For example, at only 5 weeks of age,  
67 human infants' greater relative interest in a face compared to a nonsocial object predicts lower  
68 levels of callous-unemotional traits, and greater emotion recognition and empathy, 2.5 years later  
69 (Bedford, Pickles, Sharp, Wright, & Hill, 2015). Additionally, greater attention to faces at 7  
70 months predicts children's helping behaviors at 2 years and is associated with reduced callous-  
71 unemotional traits at 4 years of age (Peltola, Yrttiaho, & Leppänen, 2018). Given the importance  
72 of social attention, and that early deviations from typical social attention may signify  
73 developmental disruptions, there is a need to better understand healthy typical development.

74 Animal models are one approach to understand social developmental disorders in humans  
75 (Bauman & Schumann, 2018; Feczko, Bliss-Moreau, Walum, Pruett, & Parr, 2016). Macaque  
76 infants are a promising NHP model, given their similarities with human infants, including strong  
77 mother-infant bonds, complex social interactions, and dedicated neural systems for social  
78 information processing (Shepherd & Freiwald, 2018). As in humans, adult macaques display  
79 privileged processing of social compared to nonsocial stimuli (Machado, Whitaker, Smith,  
80 Patterson, & Bauman, 2015; Nakata, Eifuku, & Tamura, 2018; Solyst & Buffalo, 2014; Taubert,  
81 Wardle, Flessert, Leopold, & Ungerleider, 2017), and infant macaque social attention is  
82 positively correlated with later social development. For example, male infant macaques display  
83 an increase social attention between 1 to 6 months of age, especially attention to the eye region  
84 of faces, and this increase is associated with more prosocial peer interactions between 3 to 18  
85 months of age (Ryan et al., under review). However, it remains unknown whether these social  
86 attention processes emerge through similar developmental pathways across species. To fully take  
87 advantage of animal models, it is crucial to understand whether there are similar developmental  
88 trajectories across species, both in their overall pattern, as well as in their developmental rates.

89

### 90 **Typical Developmental Trajectories of Social Attention to Dynamic Stimuli**

91 Infants' visual environments often contain numerous dynamic items competing for  
92 attention. Unfortunately, studies to date have primarily focused on infants' attention towards

93 static stimuli, and less is known about infants' attention to dynamic stimuli, the later of which  
94 may more closely approximate infants' behavior in real-world situations (Yovel & O'Toole,  
95 2016). There are a number of reasons why attention to dynamic stimuli may be different from  
96 attention to static stimuli. Most notably, dynamic stimuli may be particularly engaging, holding  
97 attention for longer than static stimuli. For example, studies presenting one video at a time report  
98 that human and NHP infants prefer to look at videos compared to photos (Livingstone, Vincent,  
99 Arcaro, Srihasam, Schade, & Savage, 2017; Ryan et al., 2019) and are more attentive when  
100 videos depict social stimuli compared to nonsocial stimuli (Frank, Amso, & Johnson, 2014;  
101 Frank, Vul, Johnson, 2008). While most studies report that human infants generally seem to  
102 display high and sometimes increasing levels of social attention to dynamic stimuli across the  
103 first months of life (Frank, Amso, & Johnson, 2014; Frank, Vul, Johnson, 2008; Hunnius &  
104 Geuze, 2004), others report that attention to dynamic social information initially declines,  
105 sometimes over the first few months (Sifre et al., 2018), the first 6 months (Courage, Reynolds,  
106 & Richards, 2006), or the first year (Libertus, Landa, and Haworth, 2017) of life, and then  
107 subsequently increases. It is theorized that attention to social stimuli may not only vary based on  
108 age, but also based on the stimuli used (e.g., static vs. dynamic; multiple stimuli competing for  
109 attention; Libertus, Landa, and Haworth, 2017). However, only a few studies in humans have  
110 directly compared infants' attention to concurrent social and nonsocial dynamic videos, and most  
111 have been with older children (Pierce, Conant, Hazin, Stoner, & Desmond, 2011; Pierce  
112 Marinero, McKenna, Barnes, & Malige, 2016). In sum, there is a need to better understand  
113 baseline levels of infant social attention longitudinally, with more complex, ecologically valid  
114 stimuli, including dynamic faces and bodies in direct competition with dynamic nonsocial  
115 stimuli (Frank, Vul, & Saxe, 2012).

116 Unfortunately, to date, there are few studies in NHP infants longitudinally examining  
117 changes in infants' attention to dynamic social and nonsocial stimuli. One study explored the  
118 effects of early experience in infant macaques reared in a neonatal nursery by human caretakers  
119 (Dettmer et al., 2016). This study found that infant macaques, at 1 month of age, spent more time  
120 observing a video of conspecifics compared to a concurrently presented nonsocial video, but  
121 only when they experienced a newborn environment with additional daily caregiver interactions  
122 beyond standard care (i.e., additional daily face-to-face interactions with mutual gaze and  
123 affiliative facial gestures). Infant macaques in another group reared with standard care (i.e.,  
124 handled every 2 hours for cleaning, feeding, and medical purposes only) did not show any social  
125 or nonsocial preferences at 1 month of age, suggesting these early social experiences may play  
126 an important role in guiding infants' attention. Further, in this study, neither group of infants  
127 showed any preference for the social or nonsocial video at 5 months, suggesting that, once the  
128 additional daily caregiver interactions ended, the effects on social attention were not long lasting.  
129 One interpretation of these results is that, unlike human infants, monkey infants may not show  
130 strong early preferences for dynamic social compared to nonsocial stimuli. However, given  
131 macaque infants' high levels of social interest with other measures, such as neonatal imitation  
132 (Ferrari et al., 2006), eye-contact (Muschinski et al., 2016), and face detection (Simpson et al.,  
133 2017), human and monkey infants may simply display different developmental trajectories of  
134 social attention that were not captured by this previous study.

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### 136 **Current Studies**

137 To begin to address these gaps, the present study sought to better understand both the  
138 potential and the limitations of macaques as an animal model of infant social attention. We

139 examined the development of social attention in macaque infants (Study 1) and human infants  
140 (Study 2) longitudinally, across the first months after birth. In both species, we used similar  
141 methods. We examined infants' visual attention to two dynamic videos played simultaneously.  
142 To gauge how interested infants were in social interactions of their own species, we chose a  
143 social video with positive, species-typical conspecific interactions, which was played  
144 concurrently with a nonsocial video that displayed a high-contrast rotating disk that moved  
145 around the screen. We choose this competing nonsocial video because it had greater low-level  
146 salience (e.g., more motion and contrast) than the social video, and thus enabled us to measure  
147 which type of stimulus—one of high social salience or one of high visual salience—attracted and  
148 held infants' attention. While infants viewed the stimuli, we tracked their visual attention with  
149 remote eye tracking.

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### 151 **Study 1: Macaque Infant Social Attention Development**

152 We examined developmental trajectories of infant macaque monkeys' visual attention to  
153 social and nonsocial videos. Compared to humans, macaques are more precocial from birth in  
154 their sensory and motor capacities, and develop more rapidly in the first year after birth,  
155 approximately four times faster (Clancy et al., 2007a, 2007b; Diamond, 1990; Teller et al.,  
156 1978). We therefore chose to test macaque infants at 1, 3, and 5 months of age to capture a wide  
157 range of early infant development approximately spanning the equivalent (in terms of perceptual,  
158 cognitive, and social development) of the first year after birth in humans.

159 We chose rhesus macaques because, like humans, they display complex social  
160 interactions in the first months after birth, including prolonged face-to-face contact with adults,  
161 with mutual-gazing, infant-directed facial gestures and vocalizations, kisses, and play (Ferrari,  
162 Paukner, Ionica, & Suomi, 2009; Dettmer et al., 2016; Simpson et al., 2018). While these  
163 similarities make macaques an intriguing model of early human development, we must be  
164 mindful of potential species differences as well. For example, studies in adult macaques suggest  
165 that they may differ from humans in their social attention (Parr, 2011; Parr, Winslow, &  
166 Hopkins, 1999). For example, a developmental study of macaque attention revealed an  
167 increasing negativity bias (a preference for negative socioemotional stimuli) across the lifespan,  
168 while humans, in contrast, display a positivity bias with age (Rosati, Arre, Platt, & Santos, 2018).  
169 Another study found, when observing videos of various social scenes, adult macaques and  
170 humans attend to different things, with humans attending more to the focus of the actions and  
171 macaques attending more to the face (Kano, Shepherd, Hirata, & Call, 2018).

172 The present study explored social attention patterns with age in macaque infants. We  
173 predicted that macaque infants would display early preferences for social relative to nonsocial  
174 videos, and that these social preferences would grow stronger with age, between 1 and 5 months.  
175 We also predicted that macaques would display a social preference earlier than humans, given  
176 macaques' more precocious development (Clancy, Finlay, Darlington, & Anand, 2007a; Clancy,  
177 Kersh, Hyde, Darlington, Anand, & Finlay, 2007b; Diamond, 1990; Teller, Regal, Videen, &  
178 Pulos, 1978).

179

### 180 *Method*

#### 181 *Participants*

182 We tested 75 macaque monkey (*Macaca mulatta*) infants (37 females) longitudinally at 1  
183 month ( $n = 75$ ; 37 females; 28-48 days,  $M = 40.55$ ,  $SD = 5.02$ ), 3 months ( $n = 55$ ; 29 females;  
184 90-112 days,  $M = 98.87$ ,  $SD = 5.72$ ), and 5 months ( $n = 74$ ; 37 females; 149-167 days,  $M =$

185 154.84,  $SD = 4.48$ ) of age. Infants were healthy, full-term, and born in 2012 ( $n = 20$ ), 2013 ( $n =$   
186 18), 2014 ( $n = 10$ ), 2015 ( $n = 16$ ), and 2016 ( $n = 11$ ). Twenty infants were not tested at 3 months,  
187 only contributing usable data at 1 and 5 months, and an additional infant was missing data at 5  
188 months. Data from a subsample of these infants were previously published (Dettmer et al.,  
189 2016); the present study expanded this sample (adding 27 new infants to the 1 and 5 month age  
190 groups;  $n = 75$ ) and tested a subset of the same infants at an additional age (3 months;  $n = 55$ ).

191 Infants were separated from their mothers on the day of birth (typically before 8am) and  
192 reared in a nursery facility by human caretakers for ongoing, unrelated research studies. This  
193 population of infant macaques, while not receiving species-typical social interactions, did receive  
194 human caregiver interactions that approximate, to some degree, the maternal care infants would  
195 receive from their biological mothers (Simpson et al., 2016a). In the first months of life, human  
196 caretakers were present for 13 hours each day and interacted with infants every 2 hours for  
197 feeding and cleaning purposes. At about 5 weeks of age, infants were placed into small, same-  
198 aged peer groups. Infants were individually housed in incubators ( $51 \times 38 \times 43$  cm) for the first  
199 two weeks of life and in larger cages ( $65 \times 73 \times 83$  cm) thereafter. Both housing arrangements  
200 contained an inanimate surrogate mother covered with fleece fabric as well as loose pieces of  
201 fleece fabric and various toys. Infants were fed Similac infant formula from birth and  
202 additionally Purina Monkey chow (#5054) starting at 2 weeks old. We introduced additional  
203 food enrichment (fruit, seeds, nuts) twice daily when infants were 2 months old. Water was  
204 available ad libitum. See Simpson, Miller, Ferrari, Suomi, and Paukner (2016b) for more details  
205 on rearing practices.

206 This population of macaques is commonly used in research studies to better understand  
207 human development (Bauman & Schumann, 2018; Wakeford et al., 2018). It is therefore critical  
208 to characterize developmental trajectories in these infants, even though studies in this population  
209 may not generalize to other NHP populations in the wild, field stations, or to laboratory animals  
210 raised in more naturalistic social groups. The *Eunice Kennedy Shriver* National Institute of Child  
211 Health and Human Development Animal Care and Use Committee approved the procedures. We  
212 conducted the study in accordance with the Guide for the Care and Use of Laboratory Animals  
213 and complied with the Animal Welfare Act.

## 214 215 Stimuli

216 One social and one nonsocial abstract video silently played side-by-side for 30 seconds  
217 (see Figure 1A and Supplementary Movie 3 in Dettmer et al., 2016; see also Ryan et al., 2019).  
218 The social video depicted macaque monkey social interactions (e.g., grooming) and was chosen  
219 because it depicted species-typical positive social behaviors. The nonsocial video included a  
220 spinning disk with orthogonal red and black stripes, rotating  $180^\circ$ , and that moved to five  
221 different locations on one side of the screen. The nonsocial video was designed to have greater  
222 low-level visual salience—including more high-contrast motion—to be particularly engaging at  
223 attracting and holding attention. The location of the videos was counterbalanced so that the  
224 social and nonsocial videos were equally likely to appear on the left and right sides of the screen.  
225 Each video was  $560 \times 320$  pixels ( $15.0 \times 8.5$  cm) and appeared on a black screen, sized  $1280 \times$   
226  $720$  pixels ( $28 \times 51$  cm). Our creation of these stimuli was inspired by a study in human children  
227 with autism spectrum disorder that played concurrent social and nonsocial dynamic stimuli  
228 (Pierce et al., 2011).

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[Figure 1 about here]

### Apparatus

We displayed the videos on a 58.4 cm monitor (28 × 51 cm) with integrated eye tracking technology. We remotely tracked infants' eye gaze via corneal reflection using Tobii T60XL ( $n = 38$ ) and Tobii TX300 ( $n = 17$ ) eye trackers, with a sampling rate of 60 Hz to be consistent with previous ongoing (unrelated) studies. Infants were tested in a room where windows with direct sunlight were blocked, and illumination of 250 lux was achieved by one overhead light (approximately 4 feet behind the infant) and one additional light to the right of the infant.

### Procedure

Infant testing took place when the infants were awake, alert, and calm. A familiar human caretaker stood in front of the eye tracker and held the infant approximately 60 cm in front of the screen (Figure 1A). Infants were swaddled at 1 month, and at 3 and 5 months were held in a fleece pouch or clung to the caretaker's arm. Before viewing the videos, each infant was first calibrated using Tobii Studio's 5 point calibration to preset locations. Calibrations of at least 3 points for each eye were deemed acceptable. Individual calibration points judged to be unreliable were repeated until acceptable. After calibration was completed, a central cartoon and music attracted the infant's attention to the center of the screen. Once the infant oriented to the center, we played the stimulus videos. Infants were free to look anywhere on or off the screen while the videos played.

### Measures

We used Tobii Studio software (Tobii Technology, Danderyd, Sweden) to collect and summarize the data. We created areas of interest (AOIs) around each video. To incorporate fixations at the edge of the stimuli, and to account for some degree of measurement error (Paukner, Johnson, & Simpson, in preparation), the AOIs were sized 632 × 578 pixels (17 × 15 cm) each, and extended over the edges of the stimuli. We used the Tobii (default) filter to extract fixations, defined as occurring within a window of 35 pixels for at least 100 ms.

We first measured infants' *total time looking* to the screen to the screen (attention holding), to test infants' overall attentiveness during the task and to test whether infants' overall attentiveness varied with age.

We next examined infants' *look latency*—how quickly infants looked to the social video versus nonsocial videos—a measure of attention capture (Simpson et al., 2017), to test whether the social or nonsocial video spontaneously captured infants' attention more readily. Then we examined how age at testing (1, 3, 5 months) predicted infants' look latency to the social and nonsocial videos to measure if there were differences in orienting speed due to age. All monkey infants made at least one fixation to each video.

Finally, for our primary analysis, we were interested in infants' relative interest in the social and nonsocial videos, so we converted look duration into the proportion of time spent looking to the social video out of the total time looking to both videos (hereafter, referred to as the *social proportion*). Our repeated measures independent variable was age at testing (1, 3, 5 months), and our final model controlled for infant sex (male, female). In an additional analysis, we tested the between subjects independent variable of cohort (year infants were born: 2014,

277 2015, 2016, 2017) to ensure that this factor was not driving our findings (see supplementary  
278 material for results).

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### 280 Data Analysis

281 For our statistical analysis, we used R version 3.4.4 and RStudio version 1.1.423 (R Core  
282 Team, 2018). We used multilevel modeling to incorporate time (i.e., infant age) as a nesting  
283 variable. We ran multilevel models within R, using the lmerTest package (Kuznetsova,  
284 Brockhoff, & Christensen, 2017) to account for dependence in our data due to nesting (repeated  
285 measures).

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### 287 Data Availability

288 The datasets analyzed during the current study are available from the corresponding  
289 author on reasonable request.

290

### 291 Results

292 We first examined if there were any age related changes in attentiveness to the screen.  
293 Macaque infants did not show any differences in total time spent looking to the screen, indicating  
294 that they were on-task, and that any differences in looking with age were not due inattention (see  
295 Supplementary Macaque Results).

296 We examined look latency to the social and nonsocial stimuli over time (with age). The  
297 fixed effect of video type was positively associated with look latency ( $\gamma_{10} = -.56, t = -2.65, p =$   
298  $.008$ ), and indicated that there was a 0.6 second decrease in look latency, on average across ages,  
299 to the social video (Figure 2a), suggesting infants were faster to look to the social compared to  
300 the nonsocial video, overall (Figure 2a). Next we examined look latency to the social stimulus by  
301 age. The fixed effect of age was positively associated with look latency to the social video ( $\gamma_{10} =$   
302  $-.41, t = -3.94, p < .001$ ), and indicated that for every month increase in age, there was a 0.41  
303 second decrease in look latency, revealing that infants' looks to the social video were getting  
304 faster over time. In contrast, for the nonsocial video we found no significant changes in look  
305 latency with age (see supplementary material for results). These results suggest that macaque  
306 infants attend first to social stimuli and, as they age, become faster to orient to social, but not  
307 nonsocial stimuli.

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[Figure 2 about here]

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311 For our primary analysis, we assessed the optimal functional form of change over time in  
312 macaque infants' social proportion. The intraclass correlation (ICC) for the random intercept  
313 model indicated that none of the variance in social proportion was explained by between infant  
314 differences. Further, the unconditional growth model with the random intercept and slope of age  
315 had an intercept variance of zero, suggesting that there was no variability among infants in the  
316 relationship between age and social proportion. A likelihood ratio test, comparing the fixed  
317 effect only model and the random effect model, indicated that there was not a significant  
318 difference between the two models ( $\chi^2(2) = 1.31, p = .519$ ). Based on a graph visualizing random  
319 slopes, there did not appear to be variability in the slopes, suggesting that there is not a random  
320 effect of age. Therefore, we removed age as a random effect. There was no significant difference  
321 in the heteroscedastic and homoscedastic model ( $p = .532$ ), suggesting that the model was  
322 homoscedastic. The macaque model contained only three time points, limiting testing of the form



323 of change over Age in social proportion to a linear model (Figure 3a).

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[Figure 3 about here]

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Our final model had an effect size of .148 indicating that the variables in our model (i.e., age and sex) explained 15% of the variance in proportion of looking relative to the unexplained variance in proportion of looking (Lorah, 2018). This is a relatively moderate effect size (Cohen 1992). The mean intercept was significantly different from zero, suggesting that, at 1 month, infants looked to the social video 47% of the time ( $\gamma_{00} = .47$ ,  $t = 20.01$ ,  $p < .001$ ). The fixed effect of age was positively associated with social proportion ( $\gamma_{10} = .04$ ,  $t = 5.71$ ,  $p < .001$ ), and indicated that for every month increase in age, there was a 0.05 increase in social proportion, revealing an increase in social proportion over time (Table 1). We found no significant effect of infant sex ( $\gamma_{01} = .003$ ,  $t = .11$ ,  $p = .909$ ). Finally, we examined social proportion compared to chance looking (i.e., looking equally to social and nonsocial videos), which revealed no preference at 1 or 3 months of age, but a preference for the social video at 5 months (Table 2).

339

### *Discussion*

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We found that macaque infants were faster to orient to the social stimulus than nonsocial stimulus, and their look latency to the social stimulus grew faster with age, between 1 and 5 months after birth; however, they showed no age-related differences in orienting speed to the nonsocial stimulus. These results suggest that dynamic social stimuli may better capture macaque infants' attention compared to nonsocial stimuli. Interestingly, this social advantage appears to grow stronger with age. These findings are consistent with previous reports for static stimuli (photos), which also found infant monkeys exhibited faster orienting to conspecific faces at 3 weeks of age, a social bias which further strengthened (grew faster) by 3 months of age, with no changes in orienting speed to objects (Simpson et al., 2017). Further, we found macaque infants looked longer to the social relative to nonsocial stimulus as they aged, in the first 5 months after birth. This linear trajectory indicates that macaques' social attention appears to be increasing consistently over the first 5 months of life. These findings are aligned with previous research in human infants that reported early social preferences and growing social attention with age (Bahrack, Krogh-Jepersen, Argumosa, & Lopez, 2014; Frank, Amso, & Johnson, 2014; Frank, Vul, Johnson, 2008; Pierce et al., 2011; Reid, Dunn, Young, Amu, Donovan, & Reissland, 2017; Valenza et al., 1996). Our results are also consistent with prior longitudinal studies in macaque infants that found early sensitivity to eye-contact, and age-related increases in looking to faces and the eyes across the first 3 months after birth (Muschinski et al, 2016; Simpson et al., 2019b; Simpson et al., 2017). While the aforementioned studies did not have a dynamic nonsocial control condition, such studies reported that both human and monkey infants displayed increasing looking times to conspecific faces with age. Our findings are also supported by a study in infant macaque monkeys tested between 10 to 60 days of age, in which brain activity was recorded with functional magnetic resonance imaging (MRI) while infants observed photos and videos depicting both social (conspecifics) and nonsocial (environmental scenes) stimuli (Livingstone et al., 2017). This study revealed that macaque infants already had neural mechanisms in place for processing social stimuli soon after birth, which rapidly developed in the first few months. While monkey infants' relative attention to social and nonsocial videos was not reported in that study, our results suggest that macaque infants display an early social attention preference, which grows stronger with age between 1 and 5 months. These ages mark

369 important social developmental transitions for macaque infants, as they become more  
370 independent from their mothers, more fully explore their early social environments, and grow  
371 increasingly socially skilled (Dettmer et al., 2016; Ferrari et al., 2009; Tomasello et al., 2001).

372 Unexpectedly, we found at 1 and 3 months of age that infant macaques appeared to look  
373 equally long to the social and nonsocial videos. This may indicate that infants at these ages do  
374 not yet show strong social attentional preferences, although we think this interpretation is  
375 unlikely given their early social attention preferences with other stimuli (e.g., Ryan et al., 2019).  
376 It is possible that our nonsocial control—the high-contrast rotating and moving disk—was  
377 simply too engaging for these young ages. That is, because the nonsocial video had higher  
378 contrast and more movement than the social video, these low-level features may have captured  
379 and held infants' attention longer. Indeed, studies in human infants suggest that younger infants  
380 are more influenced by low-level, physical salience, in visual stimuli, whereas older infants are  
381 more influenced by higher-level social relevance (Kwon, Setoodehnia, Baek, Luck, & Oakes,  
382 2016; Simpson et al., 2019c). Further studies with a wider variety of social and nonsocial videos  
383 will be necessary to more fully test this hypothesis. Nonetheless, we found that infant monkeys,  
384 by 5 months, looked longer to the social video, despite these salient low-level features, and  
385 overcame their initial bias towards low-level salience, to instead attend longer to the more  
386 socially relevant information.

387 One limitation of the present study is that these infant macaques did not experience  
388 species-typical early social environments. Given that these infants were reared in a nursery by  
389 human caretakers, and had conspecific interactions only with other infants of similar age, but not  
390 adults of their own species, this is likely to have had an effect on their early social development  
391 (Simpson, Suomi, & Paukner, 2016c). Future studies should test infant macaques who grow up  
392 in more species-typical rearing environments to determine the generalizability of our results. To  
393 this end, recent advancements in infant NHP eye tracking methods now enable researchers to  
394 capture infant NHP attention without disrupting their natural social groups. For example,  
395 researchers can remotely track infant macaque gaze patterns while they remain clinging to their  
396 biological mothers (Muschinski et al., 2016), by placing them into a box with a peep-hole for  
397 viewing stimuli (Ryan et al., 2019), or, when they are young (7 to 30 days after birth), swaddling  
398 them and having a human caretaker hold them (Paukner, Slonecker, Murphy, Wooddell, &  
399 Dettmer, 2018). Future studies using one or more of these approaches can help to disentangle the  
400 effects of specific types of early social experiences on trajectories of infant attention, to better  
401 uncover the translational value of various NHP infant populations as models for human  
402 development (Capitania, 2017; McCowan et al., 2016; Sclafani, Paukner, Suomi, & Ferrari,  
403 2015).

404

## 405 **Study 2: Human Infant Social Attention Development**

406 To better understand the relationship between healthy macaque infant social development  
407 and healthy human infant development, we carried out a second study in human infants. We  
408 examined the development of social attention in human infants using the same task and eye  
409 tracking system that we used in macaque infants, but with human (as opposed to macaque)  
410 stimuli, to directly compare development across species. The present study explored social  
411 attention patterns with age at five longitudinal time points, allowing us to examine non-linear  
412 patterns of development across the first year of life in human infants. Based on prior literature  
413 (Bahrick, et al., 2014; Frank, Amso, & Johnson, 2014; Frank, Vul, Johnson, 2008; Reid et al.,  
414 2017; Valenza et al., 1996), we expected that human infants would display early preferences for

415 the social relative to the nonsocial video, and that, although we may find an early initial decline  
416 in social attention, overall, social preferences would grow stronger with age, between 2 and 13  
417 months.

#### 418 *Method*

##### 419 Participants

420 We tested 65 human infants (24 females) longitudinally. All infants were invited to  
421 participate between 2 and 6 months of age, resulting in the following number of usable visits: 2  
422 months ( $n = 58$ ; 22 females; 54-77 days old,  $M = 63.81$ ,  $SD = 5.51$ ), 4 months ( $n = 62$ ; 23  
423 females; 113-145 days old,  $M = 126.74$ ,  $SD = 7.00$ ), and 6 months ( $n = 62$ ; 22 females; 154-200  
424 days old,  $M = 186.74$ ,  $SD = 9.09$ ). An additional subgroup of these infants also participated at 8  
425 months ( $n = 44$ ; 17 females; 233-256 days old,  $M = 246.86$ ,  $SD = 5.89$ ) and 13 months of age ( $n$   
426 = 30; 12 females; 343-443 days old,  $M = 416.03$ ,  $SD = 22.96$ ), as part of an unrelated and  
427 ongoing study. Infants were healthy, full-term ( $\geq 37$  weeks gestation), and had no parent-  
428 reported medical or vision issues. Three percent of mothers and 20% of fathers had less than or  
429 equivalent to a high school education, 64% of mothers and 54% of fathers had some college or a  
430 4-year degree, and 33% of mothers and 26% of fathers had advanced degrees. Further, 62% of  
431 families had a household income of \$50,000 a year or more. We excluded an additional 8 infants  
432 who did not attend at all to the screen either due to fussiness ( $n = 3$ ) or distraction ( $n = 4$ ), or who  
433 could not be calibrated ( $n = 1$ ). We were unable to calibrate or to track gaze on an additional 5  
434 infants at 2 months of age, so those visits were denoted as missing data.

435 The Institutional Review Board for Human Subject Research at the University of Miami  
436 approved this study.

##### 437 Stimuli

438 The video stimuli were identical to those used in Study 1, except the social video  
439 depicted two men gesturing and talking to one another in a social interaction (Figure 1B; also see  
440 Supplementary Movie 1), instead of monkeys interacting. We choose this social interaction video  
441 because it depicts a common, positive social interaction that an infant might observe. In contrast,  
442 the nonsocial video was designed to be more salient in its low-level features, having greater  
443 motion and contrast, compared to the social video. Similar to the monkey videos, the human  
444 videos were 30 seconds long, silent, and the side of the social and nonsocial videos were counter-  
445 balanced.

##### 446 Apparatus

447 The apparatus was identical to Study 1, except the Tobii TX300 sampling rate was set to  
448 300 Hz. Infants were tested in a room without windows or direct sunlight, and we achieved  
449 illumination of approximately 200 lux by using standard overhead lights.

##### 450 Procedure

451 The procedure was identical to that in Study 1, except for the following: We obtained  
452 parents' informed consent for their infants' participation. Parents completed a demographic  
453 questionnaire for each visit, which included questions about their infant's gestational age, race  
454 and ethnicity, household income, and each parent's education. All infants were seated in their  
455 parent's lap, held 60 cm in front of a screen (Figure 1B). Families were compensated \$50 for  
456 each visit.

461

## 462 Measures

463 Our dependent measures were identical to those in Study 1: *total time looking* to the  
464 screen, *look latency* to the social and nonsocial videos, and *social proportion*. Our repeated  
465 measures independent variable was age at testing (2, 4, 6, 8, 13 months), and our final model  
466 controlled for infant sex (male, female). For look latency, 11 human infants looked to only one  
467 of the two competing videos. These infants were assigned the full length of the video as their  
468 look latency value (30 seconds) to account for their non-looking (nonsocial video: seven 2 month  
469 old and two 4 month old infants; social video: one 6 month old infant and one 2 month old  
470 infant). In an additional analysis, we tested the between subjects independent variable of  
471 gestational age, parental education, and family income, to ensure that these factors were not  
472 driving our findings (see supplementary materials).

473

## 474 Data Analysis

475 Statistical analyses were performed using the same software as Study 1.

476

## 477 Data Availability

478 The datasets in the current study are available from the corresponding author.

479

## 480 Results

481 We first examined if there were any age related changes in attention to the screen. Human  
482 infants did not show any differences in time spent looking to the screen, indicating that they were  
483 on task, and that any differences in looking with age were unlikely to be due to overall  
484 inattention (see Supplementary Macaque Results).

485 Next, we conducted our look latency analysis examining stimulus type. The fixed effect  
486 of video type was positively associated with look latency ( $\gamma_{10} = -.45$ ,  $t = -4.86$ ,  $p < .001$ ), and  
487 indicated that there was a 0.45 second decrease in look latency to the social video, revealing that,  
488 pooled across ages, human infants, like monkey infants, were faster to attend to the social  
489 compared to the nonsocial video, overall (Figure 2b). In a second look latency analysis, we  
490 examined look latency to the social video as infants aged. The fixed effect of age was positively  
491 associated with look latency to the social videos ( $\gamma_{10} = -.28$ ,  $t = -2.87$ ,  $p = .005$ ), and indicated  
492 that for every month increase in age, there was a 0.28 second decrease in look latency, revealing  
493 that orienting to social videos grew faster over time. Finally, unlike macaque infants, human  
494 infants also had significant decreases in look latency to the nonsocial video as they aged ( $\gamma_{10} = -$   
495  $.71$ ,  $t = -5.74$ ,  $p < .001$ ). These results suggest that human infants attend first to social stimuli  
496 and, as they age, become faster to orient toward to both types of stimuli. For our primary human  
497 model, we assessed the optimal functional form of change over age in human infant's social  
498 proportion. The intraclass correlation (ICC) for the random intercept model indicated that only  
499 2% of the variance in social proportion was explained by between infant differences. Further, the  
500 unconditional growth model with the random intercept and slope of age had an intercept variance  
501 of .004, suggesting that there was not much variability among infants in the relationship between  
502 age and social proportion. A likelihood ratio test, comparing the fixed effect only model and the  
503 random effect model, indicated that there was no difference between the two models ( $p = 1.00$ ).  
504 Based on a graph visualizing random slopes, there did not appear to be variability in the slopes,  
505 indicating that there was no random effect of age. Therefore, we removed age as a random effect.  
506 There was a significant difference in the heteroscedastic and homoscedastic models ( $p < .001$ ),

507 so we retained the heteroscedastic model.

508 We used graphs to determine if the relationship between age and social proportion was  
509 linear or quadratic (Figure 3b). The graphs indicate that there may be a quadratic relationship,  
510 showing a decrease and then a slight increase in social proportion over time. To test this, we  
511 created a quadratic variable ( $\text{age}^2$ ) and included it in the model. We then compared this quadratic  
512 model to the linear model and found that the quadratic model was 32.57 times more likely to fit  
513 the data than the linear model, so we retained quadratic model ( $p < .001$ ). With this quadratic  
514 model,  $\text{age}^2$  was added as a random effect; however, the variation was zero, indicating that  
515 infants showed no significant differences from each other in their developmental trajectory of  
516 social looking (i.e., none of the infants diverged from the average pattern of social looking).  
517 Further, our model did not improve significantly by adding the random effect of  $\text{age}^2$  ( $p = 1.00$ ),  
518 so we moved forward with only the fixed effect of  $\text{age}^2$ .

519 Our model had an effect size of .5546 indicating that the variables in our model explained  
520 55% of the variance in proportion of looking relative to the unexplained variance in proportion  
521 of looking (Lorah, 2018). This is a relatively large effect size (Cohen 1992). The mean intercept  
522 was significantly different from zero, suggesting that, at 2 months, infants looked to the social  
523 video 66% of the time ( $\gamma_{00} = .66$ ,  $t = 14.08$ ,  $p < .001$ ). The fixed effect of age was negatively  
524 associated with social proportion ( $\gamma_{10} = -.12$ ,  $t = -8.09$ ,  $p < .001$ ), and indicated that for every  
525 month increase in age, there was a .12 decrease in social proportion, revealing a linear decrease  
526 in social proportion over time. However, the fixed effect of  $\text{age}^2$  was positively associated with  
527 social proportion ( $\gamma_{20} = .01$ ,  $t = 7.70$ ,  $p < .001$ ). For every month increase in  $\text{age}^2$ , there was a .01  
528 increase in social proportion. These results indicate that the rate of decrease in social proportion  
529 was slowing over time, as infants aged. While infants were showing a linear decrease in social  
530 looking with age, the quadratic variable of age reveals that there was a non-linear pattern of  
531 social looking: infants looked more to the social stimulus at 2 months, a social preference which  
532 decreased over time, but the rate of decrease slowed, showing an upward trend by 13 months of  
533 age. The covariate sex had no significant effect ( $\gamma_{01} = -.05$ ,  $t = -1.53$ ,  $p = .132$ ).

534 Given the quadratic effect we found, we examined a piecewise effect of age with a knot  
535 at 6 months. Similar to the previous model, we had an effect size of .5419 indicating that the  
536 variables in our model explained 54% of the variance in proportion of looking relative to the  
537 unexplained variance in proportion of looking (Lorah, 2018). The first effect of age was  
538 negatively associated with social proportion ( $\gamma_{10} = -.10$ ,  $t = -8.38$ ,  $p < .001$ ), and indicated that for  
539 every month increase in age, there was a .10 decrease in social proportion, revealing a linear  
540 decrease in social proportion from 2 to 6 months. However, the second effect of age was  
541 positively associated with social proportion ( $\gamma_{20} = .02$ ,  $t = 3.28$ ,  $p = .001$ ). For every month  
542 increase in age, there was a .02 increase in social proportion. These results indicate that social  
543 proportion was increasing from 6 to 13 months. While infants were showing a linear decrease in  
544 social looking from 2 to 6 months, there was a change in which, from 6 to 13 months, infants  
545 then showed a significant positive linear relationship with social proportion (Table 3). The  
546 covariate sex still had no significant effect ( $\gamma_{01} = -.05$ ,  $t = -1.48$ ,  $p = .143$ ). Finally, we examined  
547 social proportion compared to chance looking (i.e., looking equally to social and nonsocial  
548 videos) which revealed greater attention to the social video at 2 months, no preference at 4  
549 months, and greater attention to the nonsocial video at 6, 8, and 13 months (Table 2).

550

551 *Discussion*

552 For our initial look latency models, we found that, like macaque infants, human infants  
553 were faster to orient to the social stimulus than nonsocial stimulus, and their orienting to the  
554 social stimulus grew faster with age. These findings underscore the importance of dynamic social  
555 stimuli in capturing infants' attention, across age and across primate species. However, unlike  
556 macaque infants, human infants' look latency to the nonsocial stimulus also grew faster with age,  
557 perhaps reflecting general improvements in visual orienting speed (Canfield, Wilken, Schmerl, &  
558 Smith, 1995). Further, we found that human infants not only showed a linear decrease in the  
559 proportion of time they spent looking to social stimuli as they aged, but infants also displayed a  
560 nonlinear developmental trajectory for social looking preferences from 2 to 13 months of age. At  
561 2 months of age, human infants attended relatively more to the social than the nonsocial video.  
562 From 2 to 6 months, human infants showed a decrease in attention to the social video, yet from 6  
563 to 13 months, human infants showed an increase in attention to the social video. These results  
564 suggest that while, initially, social looking decreased in human infants, it began steadily  
565 increasing from 6 to 13 months of age. This pattern of attention indicates that human infants may  
566 display a more complex trajectory of social attention development than simply increasing with  
567 age.

568 Although much research shows an increase in social attention in human infants over the  
569 first year of life (Bahrick et al., 2014; Frank, Amso, & Johnson, 2014; Frank, Vul, Johnson,  
570 2008; Hunnius & Geuze, 2004), some literature suggests that the trajectory of social attention  
571 development is less consistent. For example, our results align with findings that infants'  
572 preference for a static social stimulus (i.e., face-shaped pattern) compared to a static nonsocial  
573 stimulus (i.e., scrambled pattern) declined from 3 to 6 months of age (Fantz, 1961). Similarly,  
574 the amount infants turned their heads to follow a static social stimulus (i.e., face-shaped pattern),  
575 compared to a static nonsocial stimulus (i.e., blank or scrambled pattern), declined from the  
576 newborn period until 5 months of age (Johnson, Dziurawiec, Ellis, & Morton, 1991). Our  
577 findings are also consistent with a cross-sectional study in human infants that reported a decrease  
578 in looking to the social compared to looking to the nonsocial dynamic stimuli from 3 to 6  
579 months, but then a rise from 6 to 12 months of age (Courage, Reynolds, & Richards, 2006). By  
580 one year of age, human infants display an overall preference for social relative to nonsocial  
581 videos (Lutchmaya & Baron-Cohen, 2002). We see a similar U-shaped pattern of development in  
582 studies examining biological motion perception in infants. For example, while infants display a  
583 preference for biological to non-biological motion at 1 month, this seems to disappear at 2  
584 months, but then reappears at 3 months and grows stronger at 24 months (Sifre et al., 2018). A  
585 similar early decline then reemerges in social attention may exist for other types of social stimuli  
586 as well, suggesting that infant social attention, in these early months, may have a more elaborate  
587 developmental pattern than merely increasing with age.

588 A limitation of the present study is that our nonsocial control—the rotating and moving  
589 disk—had higher contrast and more movement than the social video. It is possible that these low-  
590 level features captured and held infants' attention longer than the social video, which did not  
591 contain as much low-level salience. Previous studies in human infants suggest that younger  
592 infants are more influenced by low-level, physical salience, whereas older infants' attention is  
593 more influenced by higher-level social relevance. For example, one study that examined infant  
594 attention to photographs reported that 4-month-olds attended more to photos within a picture  
595 array if they had greater physical salience (e.g., high contrast, brightness) and attended less to  
596 concurrently presented faces within the same arrays, whereas older infants, by 6 to 8 months,  
597 attended more to the (more socially relevant) faces, even when in competition with physically

598 salient nonsocial photos (Kwon et al., 2016). A similar process may have occurred in the present  
599 study with our dynamic stimuli, with the upward slope in infants' social attentiveness with age,  
600 between 6 and 13 months, potentially reflecting the maturation of infants' attentional control and  
601 increases in orienting to the less physically salient but more socially relevant video. While the  
602 13-month-olds in the present study did not display a social preference, if their upward slope  
603 (growing social attention with age) continues beyond 13 months, older infants and children may  
604 show a social preference at some point before their second birthday. In future studies, testing  
605 beyond 13 months of age will help to test this hypothesis. For example, one study with 6 to 17-  
606 year old children and adolescents presented four concurrently played 15-sec videos, two social  
607 and two nonsocial, and they found that most children spent most of the time attending to the  
608 nonsocial videos (Parish-Morris et al., 2013). These authors interpreted their results as  
609 suggesting that the nonsocial stimuli were simply too salient, and highlight the need for studies  
610 using a larger number of social and nonsocial videos ranging in salience, to bring additional  
611 insights to the relative contributions of low-level and high-level stimulus attributes in guiding  
612 attention to dynamic stimuli.

613

### 614 *Species Differences*

615 Although we did not compare species directly in the previous models due to the inability  
616 to precisely match human and macaque infants on age (i.e., chronologically or developmentally),  
617 we instead pooled across ages and examined species difference in attention overall, across the  
618 first year of life (see supplementary materials for results). We found that human infants looked  
619 longer and had more fixations on average than macaque infants, suggesting that human infants  
620 may have more sustained attention than macaque infants during the first year of life. Previous  
621 studies comparing human and macaque social attention (e.g., Guo et al., 2019; Damon et al.,  
622 2017) have not directly compared species, as in the present study. In addition, we found that  
623 macaque infants spent proportionately more time looking to the social video compared to human  
624 infants, indicating that macaques' relative interest in social stimuli may be greater than human  
625 infants' relative interest in social stimuli, across the first year. Interestingly, our findings parallel  
626 findings in older ages, which report that adult humans look longer to videos than adult  
627 macaques (Kano et al., 2018); although the videos were all social, so it remains unknown  
628 whether these findings would extend to nonsocial videos, as in the present study. To our  
629 knowledge, the present study is the first report of a species difference in social attention in  
630 infancy. Further studies using a wider variety of types of stimuli and ages will be necessary to  
631 explore the generalizability these patterns.

632

633

### 634 **General Discussion**

634 It is generally accepted that, across primate species, infants display early preferential  
635 attention and processing of social stimuli, especially conspecifics (Grossman, 2015; Grossman &  
636 Johnson, 2007; Scott & Fava, 2013; Simion, Di Giorgio, & Bardi, 2011). However, our findings  
637 in the present study suggest this widely held view might be incomplete if developmental  
638 trajectories of social attention across the first year after birth are not considered. We found that  
639 macaque infants displayed growing social attention with age, from 1 to 5 months (Study 1),  
640 while human infants displayed a non-linear pattern. Human infants initially looked more to the  
641 dynamic social stimulus compared to the nonsocial stimulus at 2 months, but then showed  
642 decreased social looking from 2 to 6 months of age, instead preferring the nonsocial stimulus by  
643 6 months, followed by increased social looking from 6 to 13 months of age (Study 2). We

644 discuss potential interpretations of these linear and nonlinear developmental patterns and what  
645 these findings may indicate about healthy trajectories of social attention across species.

646

### 647 **Conspec-Conlern: Development Shift from Exogenous to Endogenous Social Attention**

648 There are several potential interpretations for our U-shaped pattern of findings in human  
649 infants, which appears in stark contrast to the macaque infants' linear pattern of increasing social  
650 attention with age. According to one model, infants' social attention in the first weeks after birth,  
651 is primarily driven by subcortical mechanisms and exogenous (automatic) social orienting, which  
652 may decline in power as infants age, while a concurrent system emerges with more cortical-  
653 based, endogenous (controlled) social orienting (for a review, see Salley & Colombo, 2016).  
654 According to this model, the initial decrease then increase that we found in human infant social  
655 attention may reflect infants' changing neural mechanisms, shifting to more endogenous  
656 (cortically-based controlled) attention (Courage et al., 2006; Johnson, Senju, & Tomalski, 2015;  
657 Morton & Johnson, 1991; Muir, Clifton, & Clarkson, 1989; Nelson, 2001). Consistent with this  
658 proposal, in a study with a variety of static and dynamic social and nonsocial stimuli presented  
659 one at a time, human infants displayed developmental increases in attention from birth to 2  
660 months of age, followed by subsequent declines in attention from 3 to 6 months of age, most  
661 notably for dynamic social stimuli (Courage, Reynolds, & Richards, 2006). While this study  
662 used a different dependent measure—peak look length—than that used in the present study, the  
663 pattern seems strikingly similar to the pattern we observed in human infants in the present study.

664 Further, this model may also explain why we failed to find this pattern in monkey infants,  
665 who we studied at a relatively more mature point in development. That is, even at only 1 month  
666 of age, a macaque infant is approximately developmentally equivalent in some areas (e.g.,  
667 sensory, motor) to that of a 4-month-old human infant. We therefore may have failed to capture a  
668 similar U-pattern of development in monkey infants, which may only be evident even earlier, in  
669 the first weeks after birth. Indeed, even more distantly related species that rely on social care,  
670 demonstrate preferences for social relative to nonsocial stimuli remarkably early. For example,  
671 newly hatched chicks selectively orient towards animate objects (Versace, Fracasso, Baldan,  
672 Dalle Zotte, & Vallortigara, 2017). Similarly in macaques, social preferences have been  
673 documented soon after birth. For example, at 2-3 weeks of age macaques prefer face-like  
674 configurations to other visual patterns (Paukner et al., 2013). Thus, it may be that future studies  
675 could examine macaque infants in the first days after birth to determine if social preferences are  
676 already present and declining across the first weeks after birth.

677

### 678 **Dynamic Systems Theory: Apparent Regression Related to Visual or Motor Development**

679 Another way to interpret our human infant U-shaped pattern of findings is within the  
680 context of dynamic systems theory, which proposes that there may be a temporary loss or  
681 reorganization of behaviors in periods of rapid transition (Gershkoff-Stowe & Thelen, 2004;  
682 Stager & Werker, 1997). According to framework, the U-shaped pattern of social attention we  
683 observed in human infants may be due to interactions with other developing systems (Cashon &  
684 Cohen, 2004; Dobson & Teller, 1978). For example, human infants' visual acuity is improving  
685 drastically during the first year after birth, perhaps overloading their system with new detailed  
686 information, leading them to process information differently, which may slow the perception of  
687 visual information until this new way of processing is more advanced, appearing, behaviorally,  
688 like the infant has regressed. Indeed, our 4- and 6-month-old human infants spent relatively  
689 longer attending to the less complex nonsocial video.



690 Additionally, human infants' peak decline in social looking preferences appears to  
691 coincide with the ability to sit independently (Cashon, Ha, Allen, & Barna, 2013), suggesting  
692 that changing human infants' point-of-view, may result in an overabundance of new perceptual  
693 information due to infants' new orientation, temporarily disorganizing information until the  
694 system adjusts to this new method of processing. Akin to visual acuity improving, motor  
695 improvements may disorganize the processing of visual information, creating preferences for less  
696 socially advanced visual stimuli, like our nonsocial video. For example, as infants' develop the  
697 ability to self-sit and reach for objects, between 3 and 6 months, they then show growing  
698 attention to objects with relatively less attention to social stimuli at these ages (Fogel, Messinger,  
699 Dickson, & Hsu, 1999; Libertus & Needham, 2011).

700 This dynamic systems approach may help explain why we do not see the same pattern in  
701 macaque infants, who develop motor skills and visual acuity around four times as fast as human  
702 infants (Diamond, 1990; Teller, Regal, Videen, & Pulos, 1978). From the day of birth, macaque  
703 infants are already able to walk, climb, and grasp objects, with fine motor coordination  
704 improvements in the newborn period (Sclafani, Simpson, Suomi, & Ferrari, 2015). Given their  
705 more precocious motor abilities at birth relative to humans, and their more rapid improvements  
706 in motor skills across the first weeks after birth, these changes may cause macaque infants even  
707 greater disorganization in their visual processing, which may explain why, in the present study,  
708 we failed to detect a preference for either the social or nonsocial videos at 1 and 3 months of age.  
709 These ages mark a period of rapid motoric and postural development in macaques. It is possible  
710 that the apparent regression we observed in human infants at 4-6 months was happening in  
711 monkey infants earlier, before 1 month of age.

712

### 713 **Clinical Implications for Studies of Typical Developmental Trajectories**

714 Indeed, in humans, there appear to be differences in infant social attention related to  
715 autism spectrum disorder (ASD; for a review: Schultz, Klin, & Jones, 2018). ASD refers to a  
716 broad range of conditions characterized in part by disruptions to social interactions. Studies have  
717 generally found that infants who go on to develop ASD, or who are at higher risk for developing  
718 ASD (due to family history), show less attention to social and more attention to nonsocial  
719 stimuli. For example, newborns at risk for ASD, compared to low-risk newborns, attended more  
720 to nonsocial relative to social visual stimuli including, biological motion (point-light displays)  
721 and faces (Di Giorgio et al., 2016). Interestingly, some ASD differences in social attention are  
722 only evident when observing infants longitudinally. For example, at 2 months, infants who later  
723 go on to develop ASD show similar patterns of social attention to infants without ASD, but  
724 between 2 and 6 months, only infants with ASD display declines in attention to the eyes (Jones  
725 & Klin, 2013). Similarly, 6-month-old infants who are later diagnosed with ASD, compared to  
726 typically developing children, attend less to a dynamic social scene (Chawarska, Macari, & Shic,  
727 2013), and 14- to 51-month-olds with ASD attend longer to a nonsocial dynamic geometric  
728 pattern than a concurrently presented social video, while typically-developing toddlers looked  
729 more instead to the social video (Franchini, Wood de Wilde, Glaser, Gentaz, Eliez, & Schaer,  
730 2016; Pierce et al., 2011; Pierce et al., 2016). Together, these studies uncover the need to better  
731 understand the development of social attention in infancy, laying the foundation for more  
732 complex, higher-level social abilities that emerge later in development.

733

### 734 **Conclusions**

735           The present study revealed that, for both macaque and human infants, there are times in  
736 early development, soon after birth, during which infants display strong preferences for dynamic  
737 social stimuli. These preferences likely reflect the importance of social stimuli for both species,  
738 critical for life in complex social groups (Arre, Clark, & Santos, 2020; Capitano, 2017; Chang &  
739 Platt, 2014; Rosati et al., 2016). We also observed some apparent species differences, namely, in  
740 the timing of when infants display preferences for social stimuli in the months after birth, and in  
741 the developmental trajectories of each species, highlighting some limitations to be mindful of  
742 when considering macaques as a model for humans. Human infants seem to show earlier  
743 preferences for a social video, attending longer to a social video already by 2 months after birth,  
744 whereas the macaque infants in this study did not appear to show a significant social preference  
745 until 5 months of age. There are a number of potential interpretations for these apparent species  
746 differences. Future research is clearly needed, tracking the development of human and NHP  
747 infants' relative interest in various types of complex, dynamic, social and nonsocial stimuli. Such  
748 studies will help to establish normative models of healthy infant development, which may  
749 provide a baseline from which infants at risk for social disruptions may be identified. In sum,  
750 while macaque infants are a valuable animal model for some aspects of human development,  
751 more research is needed in both species to understand infant developmental trajectories of social  
752 attention for macaques' translational value to be fully realized.

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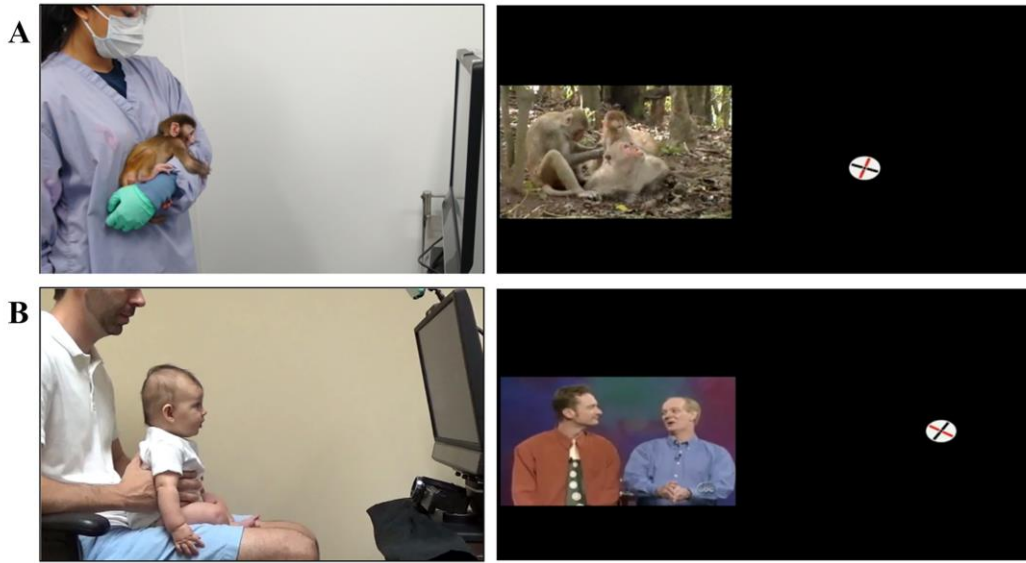
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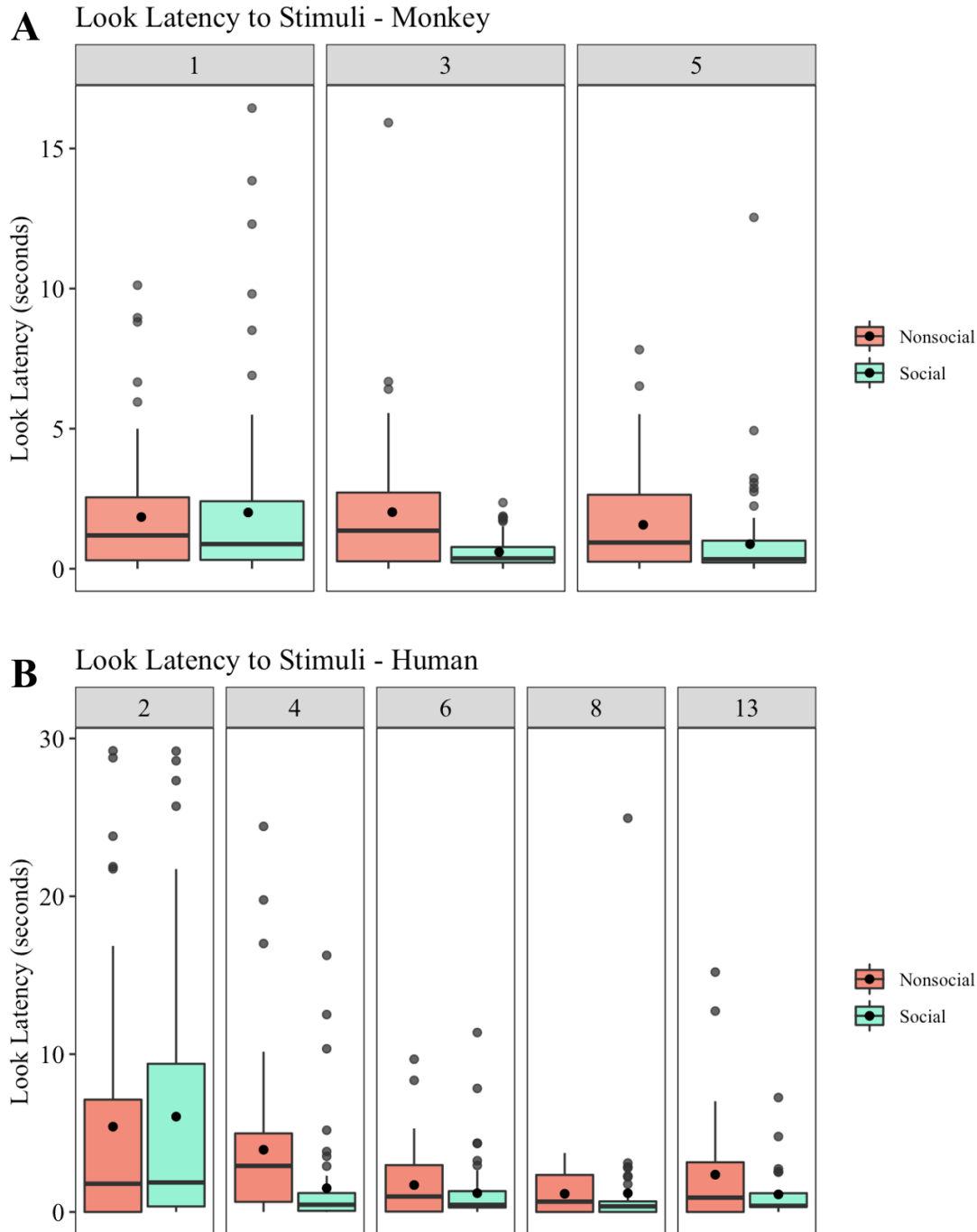
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**Figures**

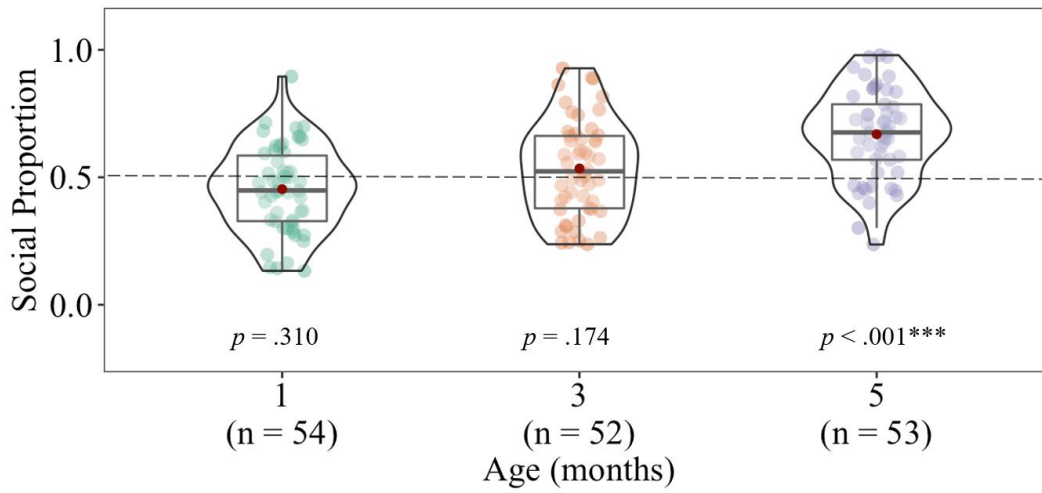
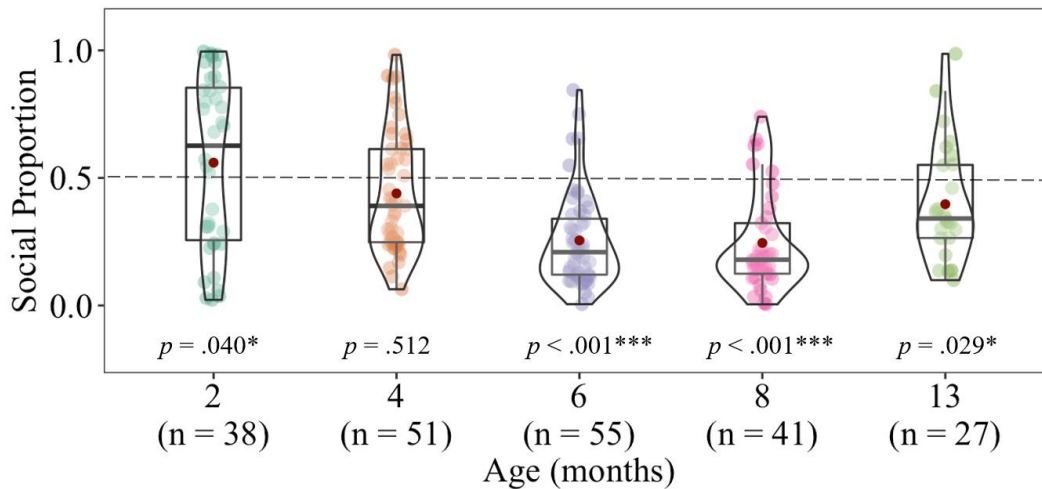


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**Figure 1.** Macaque monkey infant (A) and human infant (B) side-view of experimental testing setup (left) and sample screenshots of video stimuli (right).



1025  
 1026 **Figure 2.** Look latency to nonsocial (orange) and social (green) stimuli. Macaque monkey  
 1027 infants (A) showed a decrease in look latency to the social but not the nonsocial videos, with age,  
 1028 from 1 to 5 months. Human infants (B) showed a decrease in look latency to both the social and  
 1029 nonsocial videos with age, from 2 to 13 months. Solid horizontal lines are the medians, circles  
 1030 within each box are the means, boxes indicate 25th and 75th percentiles, respectively, whiskers  
 1031 indicate the  $1.5 \times$  interquartile range, and dots outside of the boxes indicate outliers  $>1.5 \times$  IQR.  
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**A** Social Proportion of Looks by Age - Monkey**B** Social Proportion of Looks by Age - Human

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1036 **Figure 3.** Proportion of time looking to social stimuli. Macaque infants (A) showed an increase  
1037 in social looking with age. Human infants (B) showed an initial decrease in social looking with  
1038 age, from 2 to 6 months, followed by an increase in social looking between 8 to 13 months. Solid  
1039 horizontal lines are the medians, circles within each box are the means, boxes indicate 25th and  
1040 75th percentiles, respectively, whiskers indicate the  $1.5 \times$  interquartile range, and dots outside of  
1041 the boxes indicate outliers  $>1.5 \times$  IQR. The dotted line represents chance (i.e., looking equally to  
1042 social and nonsocial videos), and the p-values indicate the difference in looking from chance,  
1043 either more to social videos (above the dotted line) or more to nonsocial videos (below the dotted  
1044 line).

1045

## Tables

**Table 1.** Macaque infant model results. \*\*\* $p < .001$ , \*\* $p < .01$ , \* $p < .05$ 

Labels	Random/Fixed	Greek Symbol	Estimate	Standard Error	$p$ -value
Intercept (b/w group)	Random Effect	$u_{0j}$	.0006		
Residual (w/in group)	Random Effect	$e_{ij}$	.0326		
Intercept	Fixed Effect	$\gamma_{00}$	.4706	.0235	< .001***
Age (w/in group)	Fixed Effect	$\gamma_{10}$	.0422	.0074	< .001***
Sex (b/w group)	Fixed Effect	$\gamma_{01}$	.0029	.0260	.909

**Table 2.** Monkey and Human infant one sample t-test comparing proportion of looking to chance (e.g., values closer to 1 represent more social looking and values closer to 0 represent more nonsocial looking). \*\*\* $p < .001$ , \*\* $p < .01$ , \* $p < .05$ 

Species	Age	Mean	95% CI	$t$ -value	$p$ -value	$d$
<b>Macaque infants</b>	1 month	.48	.41, .51	-1.02	.310	
	3 months	.53	.48, .58	1.38	.174	
	5 months	.65	.59, .70	6.70	< .001***	1.55
<b>Human infants</b>	2 months	.60	.50, .70	2.11	.040*	.58
	4 months	.48	.41, .55	-.66	.512	
	6 months	.25	.20, .30	-10.85	< .001***	-2.76
	8 months	.26	.20, .32	-8.13	< .001***	-2.45
	13 months	.41	.32, .49	-2.30	.029*	-.85

Note. Monkey and Human infant one sample t-test comparing proportion of looking to chance (i.e., looking equally between both social and nonsocial videos; a proportion of .50).

1059 **Table 3.** Human infant model results. \*\*\* $p < .001$ , \*\* $p < .01$ , \* $p < .05$   
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Labels	Random/Fixed	Greek Symbol	Estimate	Standard Error	$p$ -value
<b>Quadratic Model</b>					
Intercept (b/w group)	Random Effect	$u_{0j}$	.0061		
Residual (w/in group)	Random Effect	$e_{ij}$	.1258		
Intercept	Fixed Effect	$\gamma_{00}$	.6560	.0466	< .001***
Age (w/in group)	Fixed Effect	$\gamma_{10}$	-.1219	.0151	< .001***
Age <sup>2</sup>	Fixed Effect	$\gamma_{20}$	.0093	.0012	< .001***
Sex (b/w group)	Fixed Effect	$\gamma_{01}$	-.0522	.0342	0.132
<b>Piecewise Model</b>					
Intercept (b/w group)	Random Effect	$u_{0j}$	.0064		
Residual (w/in group)	Random Effect	$e_{ij}$	.1266		
Intercept	Fixed Effect	$\gamma_{00}$	.5874	.0518	< .001***
Age (2-6mo)	Fixed Effect	$\gamma_{10}$	-.0974	.0116	< .001***
Age (6-13mo)	Fixed Effect	$\gamma_{20}$	.0202	.0062	.001**
Sex (b/w group)	Fixed Effect	$\gamma_{01}$	-.0505	.0341	0.144