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Human and monkey infant attention to dynamic social and nonsocial stimuli

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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 nonlinear 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.

KEYWORDS

comparative psychology, gaze, infancy, nonhuman primate, sociality

1 | INTRODUCTION

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

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

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

1.1 | Typical developmental trajectories of social attention to dynamic stimuli

Infants' visual environments often contain numerous dynamic items competing for attention. Unfortunately, studies to date have primarily focused on infants' attention toward static stimuli, and less is known about infants' attention to dynamic stimuli, the latter of which may more closely approximate infants' behavior in real-world situations (Yovel & O'Toole, 2016). There are a number of reasons why attention to dynamic stimuli may be different from attention to static stimuli. Most notably, dynamic stimuli may be particularly engaging, holding attention for longer than static stimuli. For example, studies presenting one video at a time report that human and NHP infants prefer to look at videos compared to photos (Livingstone et al., 2017; Ryan et al., 2019) and are more attentive when videos depict social stimuli compared to nonsocial stimuli (Frank, Vul, & Johnson, 2009; Frank, Amso, & Johnson, 2014). While most studies report that human infants generally seem to display high and sometimes increasing levels of social attention to dynamic stimuli across the first months of life (Frank et al., 2009, 2014; Hunnius & Geuze, 2004), others report that attention to dynamic social information initially declines, sometimes over the first few months (Sifre et al., 2018), the first 6 months (Courage, Reynolds, & Richards, 2006), or the first year (Libertus, Landa, & Haworth, 2017) of life, and then subsequently increases. It is theorized that attention to social stimuli may not only vary based on age, but also based on the stimuli used (e.g., static vs. dynamic; multiple stimuli competing for attention; Libertus, Landa, & Haworth, 2017). However, only a few studies in humans have directly compared infants' attention to concurrent social and nonsocial dynamic videos, and most have been with older children (Pierce, Conant, Hazin, Stoner, & Desmond, 2011; Pierce et al., 2016). In sum, there is a need to better understand baseline levels of infant social attention longitudinally, with more complex, ecologically valid stimuli, including dynamic faces and bodies in direct competition with dynamic nonsocial stimuli (Frank, Vul, & Saxe, 2012).

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

1.2 | Current studies

To begin to address these gaps, the present study sought to better understand both the potential and the limitations of macaques as an animal model of infant social attention. We examined the development of social attention in macaque infants (Study 1) and human infants (Study 2) longitudinally, across the first months after birth.

In both species, we used similar methods. We examined infants' visual attention to two dynamic videos played simultaneously. To gauge how interested infants were in social interactions of their own species, we chose a social video with positive, species-typical conspecific interactions, which was played concurrently with a nonsocial video that displayed a high-contrast rotating disk that moved around the screen. We choose this competing nonsocial video because it had greater low-level salience (e.g., more motion and contrast) than the social video, and thus enabled us to measure which type of stimulus—one of high social salience or one of high visual salience—attracted and held infants' attention. While infants viewed the stimuli, we tracked their visual attention with remote eye tracking.

2 | STUDY 1: MACAQUE INFANT SOCIAL ATTENTION DEVELOPMENT

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

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

The present study explored social attention patterns with age in macaque infants. We predicted that macaque infants would display early preferences for social relative to nonsocial videos, and that these social preferences would grow stronger with age, between 1 and 5 months. We also predicted that macaques would display a social preference earlier than humans, given macaques' more precocious development (Clancy, Finlay, et al., 2007; Clancy, Kersh, et al., 2007; Diamond, 1990; Teller et al., 1978).

2.1 | Method

2.1.1 | Participants

We tested 75 macaque monkey (*Macaca mulatta*) infants (37 females) longitudinally at 1 month (*n* = 75; 37 females; 28–48 days, *M* = 40.55, *SD* = 5.02), 3 months (*n* = 55; 29 females; 90–112 days, *M* = 98.87, *SD* = 5.72), and 5 months (*n* = 74; 37 females; 149–167 days, *M* = 154.84, *SD* = 4.48) of age. Infants were healthy, full-term, and born in 2012 (*n* = 20), 2013 (*n* = 18), 2014 (*n* = 10), 2015 (*n* = 16), and 2016 (*n* = 11). Twenty infants were not tested at 3 months, only contributing usable data at 1 and 5 months, and an additional infant was missing data at 5 months. Data from a subsample of these infants were previously published (Dettmer et al., 2016); the present study expanded this sample (adding 27 new infants to the 1 and 5 month age groups; *n* = 75) and tested a subset of the same infants at an additional age (3 months; *n* = 55).

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

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

2.1.2 | Stimuli

One social and one nonsocial abstract video silently played side-by-side for 30 s (see Figure 1a; movie S3 in Dettmer et al., 2016; see also Ryan et al., 2019). The social video depicted macaque monkey social interactions (e.g., grooming) and was chosen because it depicted species-typical positive social behaviors. The nonsocial video included a spinning disk with orthogonal red and black stripes, rotating 180°, and that moved to five different locations on one side of the screen. The nonsocial video was designed to have greater low-level visual salience—including more high-contrast motion—to be particularly engaging at attracting and holding attention. The location of the videos was counterbalanced so that the social and nonsocial videos were equally likely to appear on the left and right sides of the screen. Each video was 560 × 320 pixels (15.0 × 8.5 cm) and appeared on a black screen, sized 1,280 × 720 pixels (28 × 51 cm). Our creation of these stimuli was inspired by a study in human children with autism spectrum disorder that played concurrent social and nonsocial dynamic stimuli (Pierce et al., 2011).

2.1.3 | 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.

2.1.4 | 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.

2.1.5 | 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, under review), 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, and 5 months)

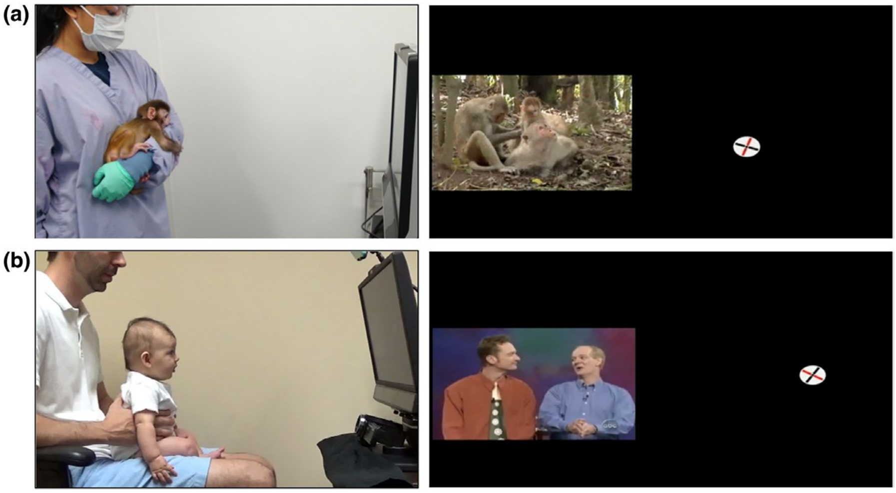

FIGURE 1 Macaque infant (a) and human infant (b) side-view of experimental testing setup (left) and sample screenshots of video stimuli (right)

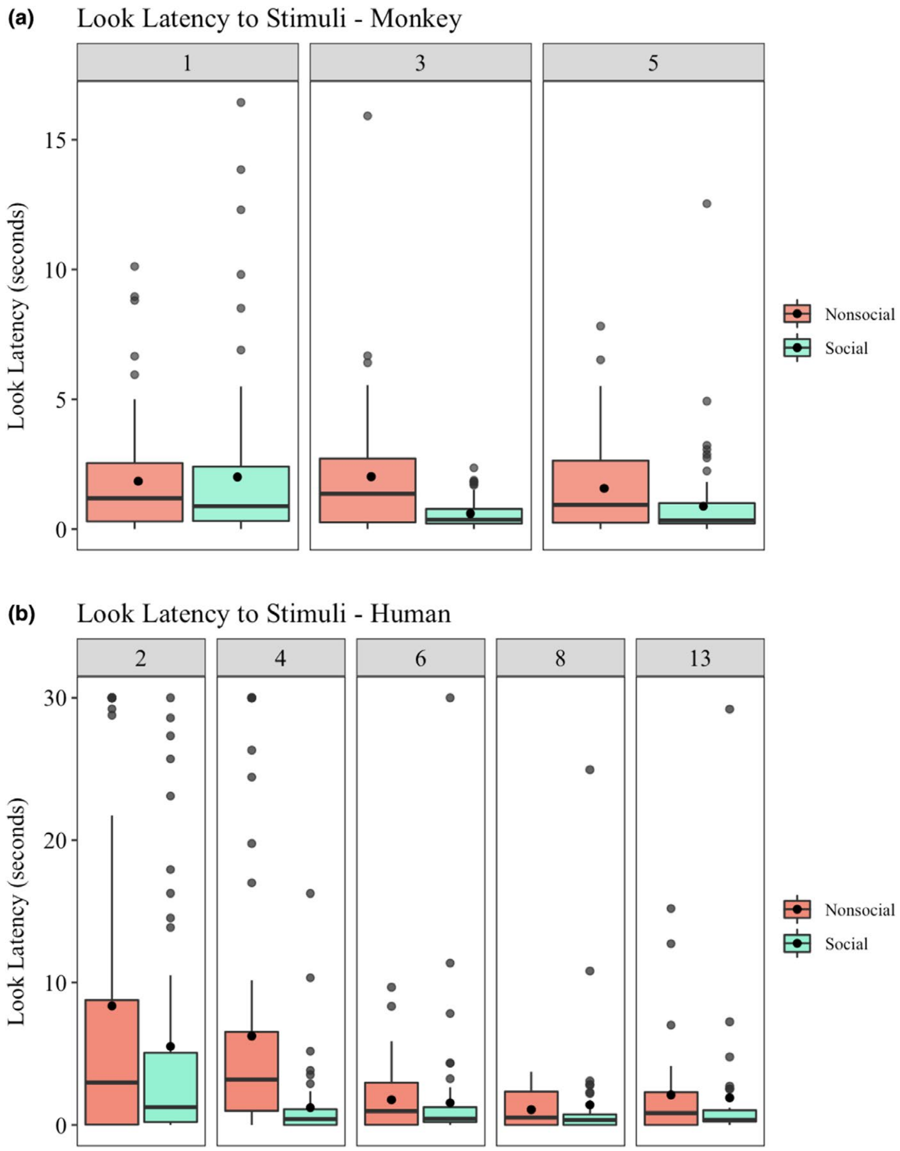

FIGURE 2 Look latency to nonsocial (orange) and social (green) stimuli. Macaque infants (a) showed a decrease in look latency to the social but not the nonsocial videos, with age, from 1 to 5 months. Human infants (b) showed a decrease in look latency to both the social and nonsocial videos with age, from 2 to 13 months. Solid horizontal lines are the medians, circles within each box are the means, boxes indicate 25th and 75th percentiles, respectively, whiskers indicate the 1.5× interquartile range, and dots outside of the boxes indicate outliers >1.5× IQR

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, and 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, 2015, 2016, 2017) to ensure that this factor was not driving our findings (see Supplementary Material for results).

2.1.6 | Data analysis

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

2.1.7 | Data availability

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

2.2 | Results

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

We examined look latency to the social and nonsocial stimuli over time (with age). The fixed effect of video type was positively associated with look latency ($\gamma_{10} = -0.56$, $t = -2.65$, $p = .008$), and indicated that there was a 0.56 s decrease in look latency, on average across ages, to the social video (Figure 2a), suggesting infants were faster to look to the social compared to the nonsocial video, overall (Figure 2a). Next we examined look latency to the social stimulus by age. The fixed effect of age was positively associated with look latency to the social video ($\gamma_{10} = -0.41$, $t = -3.94$, $p < .001$), and indicated that for every month increase in age, there was a 0.41 s decrease in look latency, revealing that infants' looks to the social video were getting faster over time. In contrast, for the nonsocial video we found no significant changes in look latency with age (see Supplementary Materials for results). These results suggest that macaque infants attend first to social stimuli and, as they age, become faster to orient to social, but not nonsocial stimuli.

For our primary analysis, we assessed the optimal functional form of change over time in macaque infants' social proportion. The intraclass correlation (ICC) for the random intercept model indicated that none of the variance in social proportion was explained by between infant differences. Further, the unconditional growth model with the random intercept and slope of age had an intercept variance of zero, suggesting that there was no variability among infants in the relationship between age and social proportion. A likelihood ratio test, comparing the fixed effect only model and the random effect model, indicated that there was not a significant difference between the two models ($\chi^2(2) = 1.31$, $p = .519$). Based on a graph visualizing random slopes, there did not appear to be variability in the slopes, suggesting that there is not a random effect of age. Therefore, we removed age as a random effect. There was no significant difference in the heteroscedastic and homoscedastic model ($p = .532$), suggesting that the model was homoscedastic. The macaque model contained only three time points, limiting testing of the form of change over Age in social proportion to a linear model (Figure 3a).

Our final model had an effect size of 0.148 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 ($\gamma_{00} = 0.47$, $t = 20.01$, $p < .001$). The fixed effect of age was positively associated with social proportion ($\gamma_{10} = 0.04$, $t = 5.71$, $p < .001$), and indicated that for every month increase in age, there was a 0.04 increase in social proportion, revealing an increase in social proportion over time (Table 1). We found no significant effect of infant sex ($\gamma_{01} = 0.003$, $t = 0.11$, $p = .909$). 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).

2.3 | Discussion

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 five 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 (Bahrick, Krogh-Jespersen, Argumosa & Lopez, 2014; Frank et al., 2009, 2014; Pierce et al., 2011; Reid et al., 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., 2017; Simpson, Paukner, Pedersen, Ferrari, & Parr, 2019). 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 and 60 days of age, in which brain activity was recorded with functional magnetic resonance imaging (fMRI) 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 important social developmental transitions for macaque infants, as

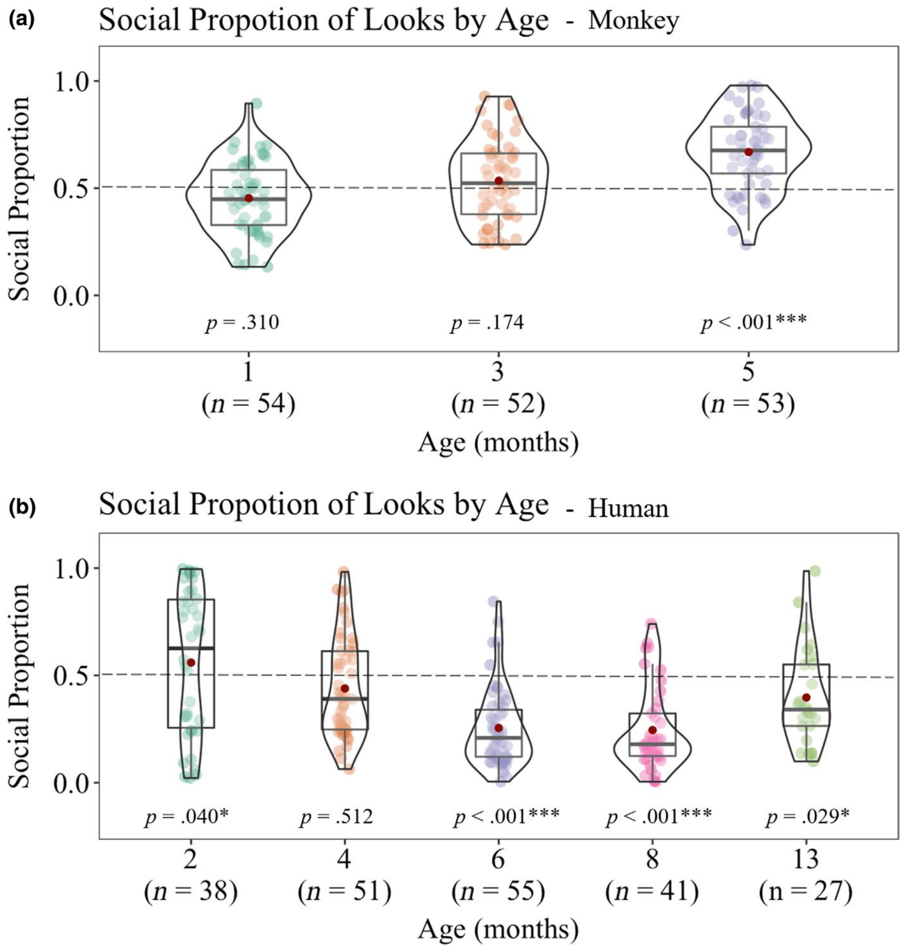

FIGURE 3 Proportion of time looking to social stimuli. Macaque infants (a) showed an increase in social looking with age. Human infants (b) showed an initial decrease in social looking with age, from 2 to 6 months, followed by an increase in social looking between 8 to 13 months. Solid horizontal lines are the medians, circles within each box are the means, boxes indicate 25th and 75th percentiles, respectively, whiskers indicate the 1.5× interquartile range, and dots outside of the boxes indicate outliers >1.5× IQR. The dotted line represents chance (i.e., looking equally to social and nonsocial videos), and the *p*-values indicate the difference in looking from chance, either more to social videos (above the dotted line) or more to nonsocial videos (below the dotted line) *ps < .05, **ps < .01, ***ps < .001

TABLE 1 Macaque infant model results

Labels	Random/fixed	Greek symbol	Estimate	Standard error	*p*-value
Intercept (b/w group)	Random effect	u_{0j}	0.0006		
Residual (w/in group)	Random effect	e_{ij}	0.0326		
Intercept	Fixed effect	γ_{00}	0.4706	0.0235	<.001***
Age (w/in group)	Fixed effect	γ_{10}	0.0422	0.0074	<.001***
Sex (b/w group)	Fixed effect	γ_{01}	0.0029	0.0260	.909

*ps < .05, **ps < .01, ***ps < .001

they become more independent from their mothers, more fully explore their early social environments, and grow increasingly socially skilled (Dettmer et al., 2016; Ferrari et al., 2009; Tomasello, Hare, & Fogleman, 2001).

Unexpectedly, we found at 1 and 3 months of age that infant macaques appeared to look equally long to the social and nonsocial videos. This may indicate that infants at these ages do not yet show strong social attentional preferences, although we think this interpretation is unlikely given their early social attention preferences with other stimuli (e.g., Ryan et al., 2019). It is possible that our nonsocial control—the high-contrast rotating and moving disk—was simply too engaging for these young ages.

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)

Species	Age	Mean	95% CI	*t*-value	*p*-value	*d*
Macaque infants	1 month	0.48	0.41, 0.51	−1.02	.310	
	3 months	0.53	0.48, 0.58	1.38	.174	
	5 months	0.65	0.59, 0.70	6.70	<.001***	1.55
Human infants	2 months	0.60	0.50, 0.70	2.11	.040*	0.58
	4 months	0.48	0.41, 0.55	−0.66	.512	
	6 months	0.25	0.20, 0.30	−10.85	<.001***	−2.76
	8 months	0.26	0.20, 0.32	−8.13	<.001***	−2.45
	13 months	0.41	0.32, 0.49	−2.30	.029*	−0.85

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 0.50).

*ps < .05, **ps < .01, ***ps < .001

TABLE 3 Human infant model results

Labels	Random/Fixed	Greek Symbol	Estimate	Standard Error	*p*-value
Quadratic model					
Intercept (b/w group)	Random effect	u_{0j}	0.0061		
Residual (w/in group)	Random effect	e_{ij}	0.1258		
Intercept	Fixed effect	γ_{00}	0.6560	0.0466	<.001***
Age (w/in group)	Fixed effect	γ_{10}	−0.1219	0.0151	<.001***
Age^2	Fixed effect	γ_{20}	0.0093	0.0012	<.001***
Sex (b/w group)	Fixed effect	γ_{01}	−0.0522	0.0342	.132
Piecewise model					
Intercept (b/w group)	Random effect	u_{0j}	0.0064		
Residual (w/in group)	Random effect	e_{ij}	0.1266		
Intercept	Fixed effect	γ_{00}	0.5874	0.0518	<.001***
Age (2–6 months)	Fixed effect	γ_{10}	−0.0974	0.0116	<.001***
Age (6–13 months)	Fixed effect	γ_{20}	0.0202	0.0062	.001**
Sex (b/w group)	Fixed effect	γ_{01}	−0.0505	0.0341	.144

*ps < .05, **ps < .01, ***ps < .001

That is, because the nonsocial video had higher contrast and more movement than the social video, these low-level features may have captured and held infants' attention longer. Indeed, studies in human infants suggest that younger infants are more influenced by low-level, physical salience, in visual stimuli, whereas older infants are more influenced by higher-level social relevance (Kwon, Setoodehnia, Baek, Luck, & Oakes, 2016; Simpson, Maylott, Leonard, Lazo, & Jakobsen, 2019). Further studies with a wider variety of social and nonsocial videos will be necessary to more fully test this hypothesis. Nonetheless, we found that infant monkeys, by 5 months, looked longer to the social video, despite these salient low-level features, and overcame their initial bias toward low-level salience, to instead attend longer to the more socially relevant information.

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

3 | STUDY 2: HUMAN INFANT SOCIAL ATTENTION DEVELOPMENT

To better understand the relationship between healthy macaque infant social development and healthy human infant development, we carried out a second study in human infants. We examined the development of social attention in human infants using the same task and eye tracking system that we used in macaque infants, but with human (as opposed to macaque) stimuli, to directly compare development across species. The present study explored social attention patterns with age at five longitudinal time points, allowing us to examine nonlinear patterns of development across the first year of life in human infants. Based on prior literature (Bahrick, et al., 2014; Frank et al., 2014; Frank et al., 2009; Reid et al., 2017; Valenza et al., 1996), we expected that human infants would display early preferences for the social relative to the nonsocial video, and that, although we may find an early initial decline in social attention, overall, social preferences would grow stronger with age, between 2 and 13 months.

3.1 | Method

3.1.1 | Participants

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

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

3.1.2 | Stimuli

The video stimuli were identical to those used in Study 1, except the social video depicted two men gesturing and talking to one another in a social interaction (Figure 1b; also see Movie S1), instead of monkeys interacting. We choose this social interaction video because it depicts a common, positive social interaction that an infant might observe. In contrast, the nonsocial video was designed to be more salient in its low-level features, having greater motion and contrast, compared to the social video. Similar to the monkey videos, the human videos were 30 s long, silent, and the side of the social and nonsocial videos were counter-balanced.

3.1.3 | Apparatus

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

3.1.4 | Procedure

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

3.1.5 | Measures

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

3.1.6 | Data analysis

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

3.1.7 | Data availability

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

3.2 | Results

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

Next, we conducted our look latency analysis examining stimulus type. The fixed effect of video type was positively associated with look latency ($\gamma_{10} = -0.45$, $t = -4.86$, $p < .001$), and indicated that there was a 0.45 s decrease in look latency to the social video, revealing that, pooled across ages, human infants, like monkey infants, were faster to attend to the social compared to the nonsocial video, overall (Figure 2b). In a second look latency analysis, we examined look latency to the social video as infants aged. The fixed effect of age was positively associated with look latency to the social videos ($\gamma_{10} = -0.28$, $t = -2.87$, $p = .005$), and indicated that for every month increase in age, there was a 0.28 s decrease in look latency, revealing that orienting to social videos grew faster over time. Finally, unlike macaque infants, human infants also had significant decreases in look latency to the nonsocial video as they aged ($\gamma_{10} = -0.71$, $t = -5.74$, $p < .001$). These results suggest that human infants attend first to social stimuli and, as they age, become faster to orient toward to both types of stimuli.

For our primary human model, we assessed the optimal functional form of change over age in human infant's social proportion. The intraclass correlation (ICC) for the random intercept model indicated that only 2% of the variance in social proportion was explained by between infant differences. Further, the unconditional growth model with the random intercept and slope of age had an intercept variance of 0.004, suggesting that there was not much variability among infants in the relationship between age and social proportion. A likelihood ratio test, comparing the fixed effect only model and the random effect model, indicated that there was no difference between the two models ($p = 1.00$). Based on a graph visualizing random slopes, there did not appear to be variability in the slopes, indicating that there was no random effect of age. Therefore, we removed age as a random effect. There was a significant difference in the heteroscedastic and homoscedastic models ($p < .001$), so we retained the heteroscedastic model.

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

Our model had an effect size of 0.5546 indicating that the variables in our model explained 55% of the variance in proportion of looking relative to the unexplained variance in proportion of looking (Lorah, 2018). This is a relatively large effect size (Cohen, 1992). The mean intercept was significantly different from zero, suggesting that, at 2 months, infants looked to the social video 66% of the time ($\gamma_{00} = 0.66$, $t = 14.08$, $p < .001$). The fixed effect of age was negatively associated with social proportion ($\gamma_{10} = -0.12$, $t = -8.09$, $p < .001$), and indicated that for every month increase in age, there was a 0.12 decrease in social proportion, revealing a linear decrease in social proportion over time. However, the fixed effect of age^2 was positively associated with social proportion ($\gamma_{20} = 0.01$, $t = 7.70$, $p < .001$). For every month increase in age^2, there was a 0.01 increase in social proportion. These results indicate that the rate of decrease in social proportion was slowing over time, as infants aged. While infants were showing a linear decrease in social looking with age, the quadratic variable of age revealed that there was a nonlinear pattern of social looking: infants looked more to the social stimulus at 2 months, a social preference which decreased over time, but the rate of decrease slowed, showing an upward trend by 13 months of age. The covariate sex had no significant effect ($\gamma_{01} = -0.05$, $t = -1.53$, $p = .132$).

Given the quadratic effect we found, we examined a piecewise effect of age with a knot at 6 months. Similar to the previous model, we had an effect size of 0.5419 indicating that the variables in our model explained 54% of the variance in proportion of looking relative to the unexplained variance in proportion of looking (Lorah, 2018). The first effect of age was negatively associated with social proportion ($\gamma_{10} = -0.10$, $t = -8.38$, $p < .001$), and indicated that for every month increase in age, there was a 0.10 decrease in social proportion, revealing a linear decrease in social proportion from 2 to 6 months. However, the second effect of age was positively associated with social proportion ($\gamma_{20} = 0.02$, $t = 3.28$, $p = .001$). For every month increase in age, there was a 0.02 increase in social proportion. These results indicate that social proportion was increasing from 6 to 13 months. While infants were showing a linear decrease in social looking from 2 to 6 months, there was a change in which, from 6 to 13 months, infants then showed a significant positive linear relationship with social proportion (Table 3). The covariate sex still had no significant effect ($\gamma_{01} = -0.05$, $t = -1.48$, $p = .143$). Finally, we examined social proportion compared to chance looking (i.e., looking equally to social and nonsocial videos) which revealed greater attention to the social video at 2 months, no preference at 4 months, and greater attention to the nonsocial video at 6, 8, and 13 months (Table 2).

3.3 | Discussion

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

Although much research shows an increase in social attention in human infants over the first year of life (Bahrick, et al., 2014; Frank et al., 2009, 2014; Hunnius & Geuze, 2004), some literature suggests that the trajectory of social attention development is less consistent. For example, our results align with findings that infants' preference for a static social stimulus (i.e., face-shaped pattern) compared to a static nonsocial stimulus (i.e., scrambled pattern) declined from 3 to 6 months of age (Fantz, 1961). Similarly, the amount infants turned their heads to follow a static social stimulus (i.e., face-shaped pattern), compared to a static nonsocial stimulus (i.e., blank or scrambled pattern), declined from the newborn period until 5 months of age (Johnson, Dziurawiec, Ellis, & Morton, 1991). Our findings are also consistent with a cross-sectional study in human infants that reported a decrease in looking to the social compared to looking to the nonsocial dynamic stimuli from 3 to 6 months, but then a rise from 6 to 12 months of age (Courage et al., 2006). By 1 year of age, human infants display an overall preference for social relative to nonsocial videos (Lutchmaya & Baron-Cohen, 2002). We see a similar U-shaped pattern of development in studies examining biological motion perception in infants. For example, while infants display a preference for biological to nonbiological motion at 1 month, this seems to disappear at 2 months, but then reappears at 3 months and grows stronger at 24 months (Sifre et al., 2018). A similar early decline then reemerges in social attention may exist for other types of social stimuli as well, suggesting that infant social attention, in these early months, may have a more elaborate developmental pattern than merely increasing with age.

A limitation of the present study is that our nonsocial control—the rotating and moving disk—had higher contrast and more movement than the social video. It is possible that these low-level features captured and held infants' attention longer than the social video, which did not contain as much low-level salience. Previous studies in human infants suggest that younger infants are more influenced by low-level, physical salience, whereas older infants' attention is more influenced by higher-level social relevance. For example, one study that examined infant attention to photographs reported that 4-month-olds attended more to photos within a picture array if they had greater physical salience (e.g., high contrast, brightness) and attended less to concurrently presented faces within the same arrays, whereas older infants, by 6 to 8 months, attended more to the (more socially relevant) faces, even when in competition with physically salient nonsocial photos (Kwon et al., 2016). A similar process may have occurred in the present study with our dynamic stimuli, with the upward slope in infants' social attentiveness with age, between 6 and 13 months, potentially reflecting the maturation of infants' attentional control and increases in orienting to the less physically salient but more socially relevant video. While the 13-month-olds in the present study did not display a social preference, if their upward slope (growing social attention with age) continues beyond 13 months, older infants and children may show a social preference at some point before their second birthday. In future studies, testing beyond 13 months of age will help to test this hypothesis. For example, one study with 6 to 17-year-old children and adolescents presented four concurrently played 15-s videos, two social and two nonsocial, and they found that most children spent most of the time attending to the nonsocial videos (Parish-Morris et al., 2013). These authors interpreted their results as suggesting that the nonsocial stimuli were simply too salient, and highlight the need for studies using a larger number of social and nonsocial videos ranging in salience, to bring additional insights to the relative contributions of low-level and high-level stimulus attributes in guiding attention to dynamic stimuli.

3.4 | Species differences

Although we did not compare species directly in the previous models due to the inability to precisely match human and macaque infants on age (i.e., chronologically or developmentally), we instead pooled across ages and examined species difference in attention overall, across the first year of life (see Supplementary Materials for results). We found that human infants looked longer and had more fixations on average than macaque infants, suggesting that human infants may have more sustained attention than macaque infants during the first year of life. Previous studies comparing human and macaque social attention (e.g., Damon et al., 2017;

Guo, Li, Yan, & Li, 2019) have not directly compared species, as in the present study. In addition, we found that macaque infants spent proportionately more time looking to the social video compared to human infants, indicating that macaques' relative interest in social stimuli may be greater than human infants' relative interest in social stimuli, across the first year. Interestingly, our findings parallel findings in older ages, which report that adult humans look longer to videos than adult macaques (Kano et al., 2018); although the videos were all social, so it remains unknown whether these findings would extend to nonsocial videos, as in the present study. To our knowledge, the present study is the first report of a species difference in social attention in infancy. Further studies using a wider variety of types of stimuli and ages will be necessary to explore the generalizability these patterns.

4 | GENERAL DISCUSSION

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

4.1 | Conspec-conlern: development shift from exogenous to endogenous social attention

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

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

4.2 | Dynamic systems theory: apparent regression related to visual or motor development

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

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

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

4.3 | Clinical implications for studies of typical developmental trajectories

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

4.4 | Conclusion

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

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

AP designed the study. AP and EAS collected the monkey infant data. EAS and SEM collected the human infant data. SEM and YAA analyzed the data. SEM, YAA, and EAS wrote the paper. All authors edited and reviewed the final paper.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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