

Effects of parity and age on female attraction to faces of infants and neonates in rhesus macaques

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Abstract This study investigated the effects of parity and age on female rhesus macaque attention toward infants, and assessed whether the faces of neonates are more attractive than those of older infants. Six nulliparous and six multiparous females were shown digitized images of neonates' and 5- to 6-month-old infants' faces. Attention and preferences for images were measured by gaze duration and other picture-directed behaviors, including lip smacking, approaches, and presentations. As predicted, nulliparous females displayed significantly longer gaze durations for images than did multiparous females. There were no significant differences in gaze duration for faces of neonates and those of infants, but images of infants were approached more frequently than images of neonates. This difference is tentatively explained on the basis of differences in female familiarity with neonates' and infants' faces and differences in opportunities for allomothering with neonates and infants.

Keywords Infant attractiveness · Females · Age · Parity · Rhesus macaque

Introduction

Sex differences in attention toward infants have been reported in many species of primates, including humans (Maestripieri and Pelka 2002). In rhesus macaques (*Macaca mulatta*), females already begin to display interest in infants in their first year of life and engage in infant handling at higher rates than males throughout their juvenile years (Lovejoy and Wallen 1988; Maestripieri 2005). If the function of early female attention toward infants is to facilitate the acquisition of mothering skills (e.g., Maestripieri and Pelka 2002), general responsiveness to infants should decline after a female has begun reproducing. This is because once females have acquired the experience to successfully raise their first offspring, continued interest in all infants (as opposed to one's own infant) will no longer be crucial for reproductive success. Consistent with this hypothesis, several human studies have shown that responsiveness to infants is greater among female children and adolescents than among middle-aged and elderly women (see Maestripieri and Pelka 2002 for a review). A similar pattern would be expected in monkeys, but variation in female attention toward infants in relation to age and parity has not been systematically investigated.

In the present study, we investigated the influence of parity and age on rhesus macaque females' attraction to infants by examining their responses to digitized images of infant faces (see Fujita 1987; Demaria and Thierry 1988; Waitt et al. 2003 for similar procedures).

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Lorenz (1943, reprinted in 1971) argued that infantile facial features (e.g., round head; protruding forehead; large eyes; and round, protruding cheeks) are specifically designed to elicit attention and caregiving behavior from other individuals. Accordingly, several human studies have shown that female children and adolescents find pictures of infant faces highly attractive (Fullard and Reiling 1976; Feldman et al. 1977; Maestriperi and Pelka 2002). Thus, in addition to testing whether nulliparous females pay greater attention toward infant faces than do multiparous females, in this study, we also investigated whether rhesus females are more attracted to the faces of neonates than to those of older infants.

Methods

Subjects

Study subjects were six nulliparous and six multiparous rhesus macaque females ranging in age from 3.94 to 19.17 years [mean age of nulliparous females = 5.65, standard error SE = 0.83; mean age of multiparous females = 13.71, SE = 2.16]. All subjects were housed in single cages at the Caribbean Primate Research Center, Sabana Seca Field Station (SSFS). Animals were required to temporarily reside in single housing due to a separate research protocol unrelated to the present study, upon completion of which animals were to be placed in social housing. The duration animals had resided in single caging ranged from 0.4 to 3.72 years (mean = 1.78 years).

Stimuli

A digital video camera (Sony DCR-PC100E) was used to capture images of 12 neonates (less than 1 week old) and of 12 infants 5–6 months old to serve as stimulus images during testing. The images were obtained from animals at SSFS who were unfamiliar to the subjects and consisted of faces with mouths closed and eyes pointed directly at the camera. Images were “frame grabbed” from digital video footage and were subsequently color calibrated in Adobe Photoshop Elements 2.0 using the RGB techniques established by Gerald et al. (2001). As it was difficult to control animals’ distance from the camera and head positioning, images were scaled and rotated to equalize interpupillary distance in order to standardize facial size and head position. All images approximated life size, and backgrounds were standardized.

Procedure

All individuals were tested during March 2005. Animals were tested within their single cages. During this time, access to both food and water was provided. Timing and display of stimuli were controlled by computer, and images appeared on a 15-in. liquid crystal display (LCD) color monitor situated 60 cm from the cage. A Spyder colorimeter and OptiCAL software (Pantone ColorVision) were utilized to color calibrate the monitor.

During the experiment, subjects were presented with a total of 24 trials of different stimulus images, 12 of which were faces of different neonates and 12 of which were faces of different infants. Order of stimuli presentation was randomized between subjects. During a trial, a single image appeared approximately life size in 24-bit color for a 10-s duration. Each trial start was controlled by the experimenter. A trial began when the animal’s eyes were orientated toward the monitor. Trials were excluded if eye gaze was obscured (i.e., females were orientated with their backs to the monitors or had their eyes closed for the entire trial). The mean number of trials per animal was 23.25, SE = 0.18 (minimum trials included = 22). Mean intertrial duration was 9.01 s (SE = 1.58). Views of the experimenter were blocked. Behavior was monitored remotely and was recorded for later analysis via a video camera placed central directly over the monitor.

The Observer software (Noldus, Version 3.0) was programmed to continuously record the subjects’ visual gaze duration and behavioral reactions to stimuli during frame-by-frame analyses. Behavioral reactions recorded included lip smacking, hindquarter presentations, and approaches. These behaviors were used as an indication of attraction to the images, along with gaze duration. Order of stimuli was unknown to the experimenter recording these data. As a single observer recorded these data, intraobserver reliability was assessed, per other studies using a single observer to assess gaze direction (e.g., Dufour et al. 2006; Fujita et al. 1997; Paukner et al. 2005). To assess this intrarater reliability, sessions from two individuals were randomly selected and reanalyzed, and then the original and reanalyzed scores were compared. Scores for gaze duration were compared in trial-by-trial correlations, yielding a reliability coefficient of 0.92 and 0.98 (Martin and Bateson 1993).

We used repeated measures analyses of variance (ANOVAs), with infant age (neonate, 5- to 6 month-old infant) as within-subjects factors and subjects’ parity (nulliparous, multiparous) as a between-subjects factor, to assess how these variables influenced gaze

duration and behavioral responses to stimuli. As it was predicted that nulliparous females would pay greater attention to stimuli, statistical analyses of parity were one-tailed. All other tests were two-tailed. Subject age was also added as a covariate, and parity and age were highly correlated ($r = 0.91$). All analyses had a significance level of $P < 0.05$ and were performed in SPSS (Version 12.0).

Results

Parity had a significant effect on gaze duration ($F_{1,10} = 3.97$, $P = 0.037$), with nulliparous females gazing longer at the stimuli than their multiparous counterparts (Fig. 1). However, when the subjects' age was added as a covariate, the effect of parity was no longer statistically significant ($F_{1,10} = 0.15$, $P = 0.370$), suggesting that age can largely explain the influence of parity on gaze duration. The subjects' parity did not significantly affect any other behavioral responses to the stimuli.

Infant age had no significant main effect on gaze duration, lip smacking, or presentations to the stimuli. Infant age, however, significantly affected the subjects' approaches to the visual stimuli ($F_{1,10} = 6.43$, $P = 0.030$), as study animals approached the images of 5- to 6-month-old infants more than images of neonates (Fig. 2).

Discussion

Nulliparous rhesus females spent significantly more time looking at digitized photos of neonates' and infants' faces than did multiparous females, as we predicted. However, it was not possible to determine

whether this effect was due to the difference in age between the subjects or to differences in parity. Here, female attraction to infants seems to decline with age, rather than decreasing abruptly after the onset of reproduction. Similar findings have been reported by studies on human females (e.g., Fullard and Reiling 1976; Maestripieri and Pelka 2002). It is possible that the decrease in attraction to infants amongst older females is the result of increasing maternal experience, consistent with the hypothesis that the function of female interest in infants is to facilitate the acquisition of mothering skills (e.g., Maestripieri and Pelka 2002). In rhesus macaques, the number of offspring, and thus maternal experience, are highly correlated with age, and teasing apart the effects of these two variables on female attraction to infants requires a larger sample size than that which was available in this study. Further studies should test age-equivalent groups of differing parity, or should be longitudinal studies, to disentangle the specific effects of parity and age.

Although infant age did not influence gaze duration or the frequency of lip smacking or presentations directed to the pictures, images of 5- to 6-month-old infants were approached more frequently than were images of neonates. This suggests that neonates are no more attractive than 5- to 6-month-old infants. Such a result is not particularly surprising given that young rhesus infants spend most of their time in ventro-ventral contact with their mother, with their faces out of view of conspecifics (Maestripieri 1995). By contrast, 6-month-old infants spend most of their time off of their mother (Hinde and Spencer-Booth 1967), thereby increasing familiarity, and thereby perhaps attractiveness, of their faces to others. Additionally, attraction to older infants may be related to opportunities for infant handling, or allomothering.

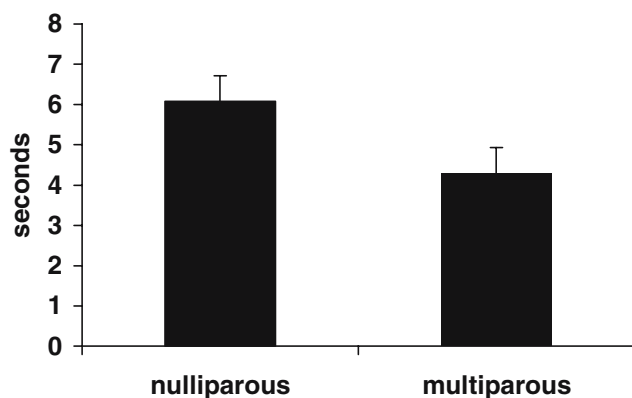


Fig. 1 Mean gaze duration (seconds) and standard error (SE) of young nulliparous females versus older multiparous females for all images (neonates and 5- to 6-month-old infants)

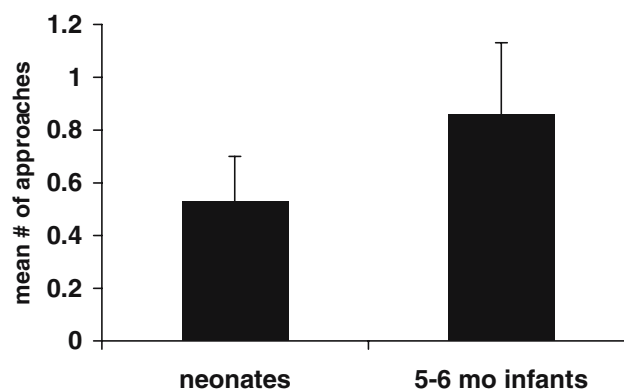


Fig. 2 Mean approach rate and standard error (SE) of all females for images of neonates versus 5- to 6-month-old infants

Amongst macaques, neonates are rarely handled by other females while older infants are more independent from their mothers and therefore more easily available to other females (Maestriperieri 1994). Thus, as approaching and handling infants may facilitate the acquisition of mothering experience, this may explain why pictures of 5- to 6-month-old infants were approached more than pictures of neonates. Additionally, the greater approach rate may be a result of it generally being safer to approach older infants, as neonates can be aggressively guarded by their mothers (Maestriperieri 1994).

The experimental paradigm used in this study is a promising approach for the investigation of social preferences of nonhuman primates. The use of digitized images can improve our understanding not only of individual differences in attraction to social stimuli but also the identification of the specific features of these stimuli that make them attractive. However, there are also some potential shortcomings. It should be noted that no significant difference was found in behavioral reactions, including approaches, among nulliparous or multiparous females, which seems somewhat contradictory in light of differences in gaze duration. The reason for the lack of difference is not entirely clear, but it is possible that this could result from the lack of interactivity of the pictorial stimuli, and such limitations should be considered by anyone using this testing paradigm.

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