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An experimental examination of female responses to infant face coloration in rhesus macaques

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Abstract

In many primates, infants possess distinctive coloration that changes as a function of age. This colour is thought to serve the purpose of eliciting caretaking behaviour from the mother as well as other conspecifics. The present study investigated the responses of adult female rhesus macaques (*Macaca mulatta*) to pictures of infant faces in relation to infant age and facial coloration. Study animals were shown digitized images of neonates and 5–6-month-old infants displaying either unaltered facial colour, pink neonatal colour, or novel (green) facial colour. While infant and neonate faces of all colours elicited the attention of adult females, pink neonatal facial coloration did not appear to be especially attractive to subjects in contrast with the findings from an earlier study [Higley, J.D., Hopkins, W.D., Hirsch, R.M. Marra, L.M. Suomi S.J., 1987. Preferences of female rhesus monkeys (*Macaca mulatta*) for infantile coloration. Dev. Psychobiol. 20, 7–18]. The results suggest that infant facial colour is not particularly important in mediating infant attractiveness to rhesus macaque females as previously suggested or that other infantile facial characteristics might be more important than colour in eliciting caretaking behaviours amongst females.

Keywords: Natal facial colour; Infant; Primate; Rhesus macaque

1. Introduction

In many animal species including humans, infants display age-specific morphological and behavioural features that make them attractive to adults. For example, (Lorenz 1943, reprinted in 1971) argued that infantile facial features, such as round heads, protruding foreheads and large eyes are specifically designed to elicit interest and caregiving behaviour from other individuals. In addition to their particular facial features, the infants of many primate species also possess a distinctive skin or coat coloration (e.g., pink or blue facial skin, orange or black coat). The hypothesis that infantile coloration is attractive to conspecifics (Alley, 1980; Horwich and Gebhard, 1986; Hrdy, 1976; Treves, 1997; Ross and Regan, 2000) has rarely been tested, with the exception of a single study of rhesus macaques in which infantile facial and coat coloration were artificially manipulated (Higley et al., 1987).

Rhesus macaque infants are born with pink facial skin coloration, which fades within a few days or weeks, and a coat coloration that is slightly darker than that of adults in the first 6 months of life. Using the experimental apparatus developed by Sackett et al. (1967), Higley et al. (1987) examined female rhesus macaque attraction to 6-month-old infants whose faces or coats were artificially dyed to simulate neonatal coloration versus infants with faces and coats unaltered for coloration. The females did not exhibit consistent preferences for infant coat coloration, but spent more time near infants with pink facial skin. This effect was not due to novelty, as females spent relatively little time near infants whose faces had been dyed green. Females showed preferences for pink-faced infants were shown by females regardless of their own rearing history (wild-born versus lab-born, mother-reared versus hand-reared) or reproductive condition (pregnant versus non-pregnant). Although these results are consistent with the hypothesis that the coloration of newborns' faces is attractive, it is also possible that rhesus females are generally more attracted to neonates than to older infants, and that the subjects in the Higley et al. (1987) study showed a preference for infants with pink faces because

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their faces made them appear younger, as the authors suggest.

In the present study we experimentally investigated the responses of rhesus macaque females to infant faces to assess the extent to which infant attractiveness is due to facial coloration or other age-specific features. Unlike the Higley et al. (1987) study in which live infants were used, we used digitized photos of infant and neonate faces as stimuli and measured gaze duration as our main measure of interest (see Fujita, 1987; Fujita et al., 1997; Demaria and Thierry, 1988; Waitt, 2005; Waitt and Little, in press, for similar procedures). The use of digitized photos of infant faces offers several advantages, including the opportunity to investigate face attractiveness in isolation from other physical or behavioural cues, and the opportunity to perform a precise and realistic manipulation of face coloration. In addition, testing the animals under these standardized experimental conditions increases the extent to which the results can be replicated and generalized, and eliminates possible physical injury or stress caused by the use of live animals.

2. Materials and Methods

2.1. Study animals

Study animals were 12 female adult rhesus macaques (six nulliparous and six multiparous females), all housed in single cages (77 cm $H \times 61$ cm $W \times 61$ cm D) at the Caribbean Primate Research Center, Sabana Seca Field Station (SSFS). Single housing was required for these animals by a separate research protocol unrelated to the present study, after which animals were to be placed in social housing. Subjects ranged in age from 3.94 to 19.17 years (mean age = 10.18, S.E. = 1.71).

2.2. Stimuli

A digital video camera (Sony DCR-PC100E) was used to capture images of 12 neonates (less than 1 week of age) and of 12 infants 5–6 months in age to serve as visual stimuli. 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 colour calibrated in Adobe Photoshop Elements 2.0 using the RGB techniques established by Gerald et al. (2001).

To manipulate coloration, we adapted the computer graphics techniques used by Rowland and Perrett (1995) to alter human facial coloration. These techniques have been successfully employed in three previous studies examining conspecific response to altered secondary sexual coloration among rhesus macaques (Gerald et al., in press; Waitt et al., 2003; Waitt et al., 2006). A composite face was produced by creating i.e. creating computerized amalgamations of images of six additional neonates exhibiting pink facial coloration. Multiple images of different individuals were used to form composites to control for individual differences in coloration. To construct the composite, the mean RGB colour values at each pixel were calculated for the sample and these were transformed into hue and saturation values. Hue and saturation values were then applied and combined with the individual brightness component of each pixel of the 24 stimulus faces, producing a pink version of each face (see Rowland and Perrett, 1995 for further details). To create a novel facial colour condition, Adobe Photoshop Elements 2.0 was employed to change the facial colour of six faces to green, from which a composite was formed and the same procedure as above was utilized to apply this colour to the stimulus faces. To standardise face size and head position, images were scaled and rotated to equalise inter-pupillary distance. All images approximated life-size and backgrounds were standardized across images by cropping and placing faces against the same colour calibrated naturalistic background image taken on the island of Cayo Santiago, in an attempt to create a natural contrast to stimuli, as recommended when using artificial visual stimuli to investigate the significance of colour in animal communication (Fleishman and Endler, 2000).

2.3. Procedure and equipment

All experiments took place in the home cages of study animals. Animals were provided access to both food and water on an ad libitum basis. A 15 in. LCD colour monitor, located 60 cm from the cage projected images, and the timing and display of stimuli were controlled by computer. In order to achieve colour consistency of images, a Spyder™ colorimeter and OptiCAL software (Pantone ColorVision) were implemented to calibrate the monitor colour.

For each experimental trial, subjects were presented with a total of 24 stimulus face images, of which 12 were of faces of different neonates and 12 were faces of different infants. The images of stimulus neonates and infants were altered to create a pink and green condition for each face. Order of stimuli was randomized and presentation of unaltered, pink and green versions of each face was counterbalanced between subjects (i.e., animals viewed each face only once, in one of the three colour conditions; for example, a face seen in the pink condition by one subject would be seen as unaltered by a second subject, and in the green condition by a third subject).

Behaviour was recorded via a video camera, placed directly over the monitor in a central location. As soon as the study animal’s eyes were oriented towards the monitor, a trial began. During a trial, a single image appeared in 24-bit colour for 10 s duration. Trials were discarded if eye gaze was obscured (i.e., backs were facing the monitor or eyes were closed for the entire trial). The mean number of trials per animal was 23.25 (minimum trials included = 22, S.E. = 0.18).

2.4. Behavioural observations

The Observer software (Noldus, Version 3.0) was programmed for continuous focal recording (Martin and Bateson, 1993) of the subjects’ visual gaze duration and behavioural reactions to stimuli, during frame-by-frame analyses. While the Higley et al. (1987) study measured caretaking behaviours of females directed toward young stimulus animals, our use of digital stimuli precluded the occurrence of these behaviours.

Instead, behavioural reactions recorded here included: lipsmacking, hindquarter presentations, and approaches, as these behaviours can be used as an indication of interest and attraction. Presentation order of stimuli was unknown to the experimenter recording these data. To assess intra-observer reliability, sessions from two individuals were randomly selected and re-analyzed, and then the original and re-analyzed 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).

2.5. Statistical analyses

We used repeated measures ANOVAs, including infant colour (unaltered, pink, green) and age (neonate, 5–6-month-old infant) as within subjects factors to assess how these variables influenced gaze duration and behavioural responses to stimuli. Given the empirical precedence, we predicted that females would prefer pink neonatal coloration; thus, statistical analyses of colour were one-tailed. All other tests were two-tailed. All analyses had a significance level of $p < 0.05$, and were performed in SPSS Version 12.0.

3. Results

Contrary to our predictions, colour had no significant main effect on gaze duration ($F_{2,22} = 0.10$, $p = 0.904$; Fig. 1), lipsmacking ($F_{2,22} = 0.67$, $p = 0.523$), or presentations ($F_{2,12} = 1.10$, $p = 0.365$). Similarly, infant age had no significant main effect on gaze duration, lipsmacking, or presentations to the stimuli. Infant age, did however, significantly affect the subjects' approaches to the visual stimuli (two-tailed: $F_{1,11} = 5.71$, $p = 0.038$), with images of 5–6-month-old infants being approached more than those of the neonates (Fig. 2). There was also a significant interaction between infant colour and infant age on female approaches to stimuli ($F_{2,20} = 3.75$, $p = 0.041$; Fig. 2), such that the images of pink and unaltered neonates were approached less than those of pink and unaltered infant counterparts (Fig. 2). However, after making Bonferroni probability adjustments (0.05/2 = 0.025), the post-hoc two-tailed paired *t*-tests only approached statistical significance (pink neonates versus pink infants: $t = 2.55$, $p = 0.027$; unaltered neonates versus unaltered infants: $t = 1.87$, $p = 0.089$).

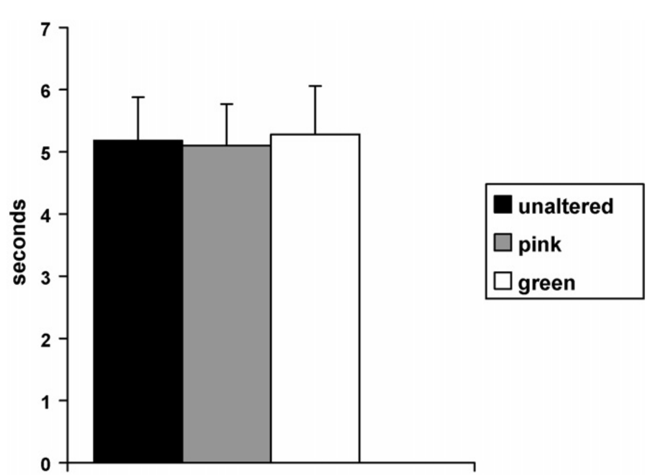

Fig. 1. Mean gaze duration (seconds) and S.E. of females for all images (both neonates and 5–6 month-old infants) by color (unaltered, pink, green).

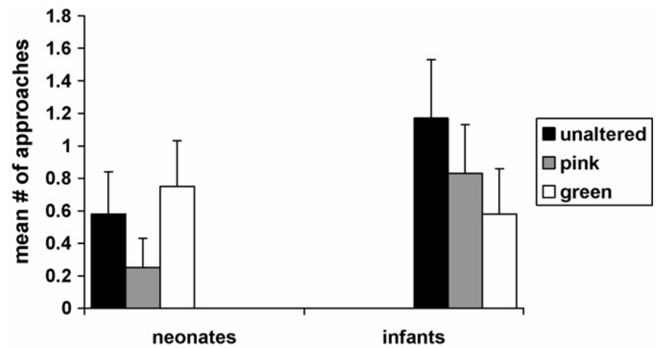

Fig. 2. Mean number of approaches and SE of all females for images of unaltered, pink, and green neonates vs. 5–6-month-old infants.

While 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, when analyses included the subjects' age as a covariate, the effect of parity was no longer statistically significant ($F_{1,10} = 0.15$, $p = 0.370$). This suggests that age drove the effect of parity on gaze duration. Parity did not significantly impact any other behavioral responses to the stimuli.

4. Discussion

Infant face coloration had no significant main effect on female gaze duration. Although the age of the stimulus animals did not influence gaze duration, it did affect the frequency of female approaches to pictures. Images of 5–6-month-old infants were approached more frequently than those of neonates. There were no significant differences in lipsmacking or presentations directed to the pictures, irrespective of the age or face coloration of the stimuli. These findings suggest that the pink face coloration of rhesus neonates is not especially attractive to rhesus females and, more generally, that females do not find neonates more attractive than 5–6-month-old infants.

The absence of strong effects of neonatal facial coloration on attractiveness may be due to the fact that neonatal coloration in our rhesus macaque population fades by 7–10 days after birth (CW, MG, personal observation) and that during this period, rhesus infants spend most of their time in ventro-ventral contact with their mother, with their faces pressed against their mothers' chests (Maestripieri, 1995). Therefore, neither mothers nor other females are as extensively exposed to the pink faces of neonates in comparison to 5–6-month-old-infants, who spend most of their time out of contact with their mothers (Hinde and Spencer-Booth, 1967). Thus, we speculate that rhesus macaque females are probably exposed to faces of infants more than to faces of neonates and generally have more opportunities to interact with infants than with neonates. The attractiveness of infant faces, however, is likely to depend on features other than colour (e.g., rounded shape, large eyes).

Although the use of images as visual stimuli does not allow us to make strong inferences about the social preferences of rhesus females for neonates versus infants, it did allow us to investigate the relative importance of facial coloration and age for infant attractiveness under controlled experimental conditions. In particular, digital manipulations of images such as the ones used in the present study allow for consistency, as there is complete control over artificial coloration. It is possible that Higley et al. (1987) were unable to achieve consistency in the artificial coloration or, alternatively, their subjects may have keyed into other colour-based signals salient to rhesus macaques. For example, male and female rhesus macaques experience reddening of the sexual skin during the mating season (Baulu, 1976), and pregnant rhesus macaque coloration turns near magenta immediately prior and following parturition (Czaja et al., 1975).

Alternatively, the pink coloration of a neonate's face may not serve any signalling function but could simply be a physiological epiphenomenon, such as a by-product of blood oxygenation, lacking adaptive significance. It may also be possible that females could use neonatal colour as a cue to infant health; in a prospective study of human newborns, colour was an indicator of infants at high risk for severe morbidity (De Felice et al., 2002). However, our data do not support this hypothesis, as females did not appear to preferentially attend to images of neonates based on colour.

Our experimental design limits us from evaluating all of these alternatives. More experimental tests of infant attractiveness with a broader range of stimuli would be necessary to address these questions. Testing the attention and behavioural responses of nonhuman primates to relevant social stimuli can elucidate what features are salient to conspecifics. These tests can assist us in determining the role of social stimuli in communication. The experimental paradigm used in this study can allow for the experimental manipulation of individuals' physical characteristics and the assessment of responses to these manipulations in a controlled laboratory setting. Future studies using this paradigm can further examine what physical signals and cues are salient to nonhuman primates, as well as their knowledge of their social and physical world.

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