

BRIEF REPORT

Selective Attention Toward Female Secondary Sexual Color in Male Rhesus Macaques

CORRI WAITT^{1–3}, MELISSA S. GERALD^{1,2*}, ANTHONY C. LITTLE⁴,
AND EDMUNDO KRAISEL BURD²

¹Cayo Santiago, Caribbean Primate Research Center, Punta Santiago, Puerto Rico

²Department of Medicine, Medical Sciences Campus, University of Puerto Rico, San Juan, Puerto Rico

³Scottish Primate Research Group, Department of Psychology, University of Stirling, Stirling, United Kingdom

⁴School of Biological Sciences, University of Liverpool, Liverpool, United Kingdom

Pink-to-red anogenital and facial sexual skin occurs in females of many primate species. Since female sexual skin color varies with reproductive state, it has long been assumed that color acts to stimulate male sexual interest. Although there is supportive evidence for this as regards anogenital skin, it is unclear whether this is also the case for facial sexual skin. In this study we experimentally manipulated digital facial and hindquarter images of female rhesus macaques (*Macaca mulatta*) for color within the natural range of variation. The images were presented to adult male conspecifics to assess whether the males exhibited visual preferences for red vs. non-red female coloration, and whether preferences varied with anatomical region. The males displayed significantly longer gaze durations in response to reddened versions of female hindquarters, but not to reddened versions of faces. This suggests that female facial coloration may serve an alternative purpose to that of attracting males, and that the signal function of sexual skin and the intended recipients may vary across anatomical regions. *Am. J. Primatol.* 68:738–744, 2006. © 2006 Wiley-Liss, Inc.

Key words: secondary sexual color; female sexual skin; primate; *Macaca mulatta*

INTRODUCTION

Female primates of many species possess regions of anogenital and facial “sexual skin” that vary in color in relation to reproductive state. Changes in sexual skin color are regulated by ovarian estrogen [e.g., Czaja et al., 1977; Herbert, 1966], which acts to increase vascular blood flow under the skin surface

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*Correspondence to: Dr. Melissa S. Gerald, Cayo Santiago, Caribbean Primate Research Center, P.O. Box 906, Punta Santiago, PR 00741. E-mail: mgerald@rcm.upr.edu

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and thus induces pink-to-red coloration [reviewed in Dixson, 1998]. In some species (e.g., mangabeys (*Cercocebus* spp.) and some macaques (*Macaca* spp.)), female anogenital skin color changes across the ovulatory cycle, reddening during the follicular phase, peaking in color in the periovulatory period, and then decreasing in the luteal phase; however, the relationship with ovulation is not fixed [Dixson, 1983]. Other species exhibit anogenital reddening during ovulatory cycles, but color varies little across the cycle (e.g., Japanese macaques (*M. fuscata*) [Wallner et al., 2002]). Similarly, female facial reddening may occur while females are fertile, but this tends not to vary across the cycle in most species (e.g., Japanese macaques [Wallner et al., 2002], rhesus macaques (*M. mulatta*) [Baulu, 1976], and toque macaques (*M. sinica*) [Dittus, 1975]).

The color of female sexual skin has long been thought to play a role in stimulating male sexual interest. Despite this long-held assumption, the role of color in mediating female attractiveness has only been investigated experimentally in one study by Bielert and colleagues [1989]. In that study an ovariectomized female chacma baboon (*Papio ursinus*) was fitted with artificial sexual swellings that differed in color (e.g., black, green, white, and red), and the red swelling elicited the greatest male masturbatory response. This led the authors to conclude that the color red acts as a sexual releaser for male primates. Whether this is also the case for red facial sexual skin is unclear, since no published experimental studies have addressed female facial color. It is possible that the functions of sexual skin color vary across anatomical regions, and thus males may have a preference for red coloration in only certain traits rather than a general red preference. Evidence from other species with multiple secondary sexual ornaments suggests that different ornaments may provide receivers with information on separate aspects of condition and behavior (e.g., northern cardinals (*Cardinalis cardinalis*) [Jawor & Breitwisch, 2004]), and that different ornaments have evolved to convey messages to different receivers (e.g., widow-birds (*Euplectes ardens*) [Andersson et al., 2002]).

In free-ranging rhesus macaques, adults of both sexes exhibit increased facial and anogenital skin reddening during the mating season. In the present study we experimentally manipulated facial and hindquarter female rhesus macaque images for color. We predicted that if female face and hindquarter reddening indeed acts as attractant to males, then males should exhibit visual preferences for red female coloration across anatomical regions.

MATERIALS AND METHODS

Study Animals

The study animals were 20 male adult rhesus macaques (mean age = 14.83 years, SD = 5.40 years) that were singly housed outdoors at the Caribbean Primate Research Center, Sabana Seca Field Station (SSFS). Eighteen of the subjects originated from the free-ranging population of Cayo Santiago and were removed as a population control measure, whereas the remaining two were born and reared at SSFS in harem groups. None of the animals had previously been exposed to pictorial stimuli. One individual was dropped from the study due to inattention to stimuli. The animals were tested during October 2005 and March 2006. All of the procedures used in this study were approved by the UPR Institutional Animal Care and Use Committee (IACUC). Although the mating peak occurs from September to February at SSFS, mating takes place throughout the year, and therefore no strict mating vs. nonmating periods exist that may otherwise mediate male attention.

Stimuli

A digital video camera (Sony DCR-PC100E) was used to capture images of 24 individual female rhesus macaques at SSFS. Facial images were taken while the animals exhibited neutral expressions, with mouths closed and faces and eyes pointed directly at the camera. Since the images showed direct gaze, they may not have been perceived as expressionally neutral, because prolonged eye contact is associated with aggressive intent [Hinde & Rowell, 1962]. However, macaques also use different facial attributes (e.g., mouth configuration and brow position [Perrett & Mistlin, 1990]) to interpret intent. Eye contact also occurs in other communicative contexts (e.g., appeasement gestures [van Hooff, 1967] and sexual solicitations [Dixon, 1998]). Controlling for eye gaze direction was essential because it can influence looking behavior [e.g., Sato & Nakamura, 2001]. Hindquarter images were taken directly from behind while the animals were standing with tails erect, exposing the entire anogenital and surrounding regions of the sexual skin. Images were “frame grabbed” from digital video and downloaded onto a computer (Sony Vaio V505 series) as 640×480 pixel images in jpeg format. All images were color calibrated in Adobe Photoshop Elements 2.0 using the red-green-blue (RGB) methods [Gerald et al., 2001].

To manipulate coloration, we adapted computer graphics techniques used to alter human facial color (see Rowland and Perrett [1995] for details). We constructed two composite faces (a red face and a non-red face) by creating computerized amalgamations of eight of the reddest and eight of the least-red images. Multiple images were used to control for individual differences in coloration, and differences in ambient lighting. To make composites, we calculated the mean RGB color values at each pixel for the sample and transformed them into hue and saturation values. Hue and saturation values were then applied and combined with the individual brightness component of each pixel of eight individual female stimulus faces (from the eight individuals of intermediate color range, not used in the composites), to produce a red and a non-red version of each face. The same procedure was followed to transform hindquarter coloration. All color manipulations were within the natural range of variation, but since these techniques combine the applied hue and saturation with the existing values, there was a small degree of variation among stimuli of the same color category. We standardized the backgrounds across images by cropping and placing the faces and hindquarters against the same color-calibrated background image taken on Cayo Santiago. This was done in an attempt to create a natural contrast to the stimuli, as is recommended when using artificial visual stimuli to investigate the significance of color in animal communication [Fleishman & Endler, 2000].

Procedure and Equipment

The males were moved to the testing area (adjacent to their living quarters) in their single cages by caretakers. The animals were habituated to the testing area for 1–3 hr before they were tested. During that time the animals were provided access to both food and water. Testing took place from 1500 to 1700 hr after all feeding and cleaning routines were completed.

A SpyderTM colorimeter and OptiCAL software (Pantone ColorVision) were utilized to color calibrate the monitor weekly to ensure realistic and consistent color depiction. During testing the experimenter was situated directly behind the monitor; however, views of the experimenter were blocked with a curtain.

Attention to Female Secondary Sexual Color / 741

Behaviors were monitored remotely and recorded for later analysis via a digital camera that was placed central directly above the monitor, and a laptop computer. A trial began when the animal's eyes were oriented toward the monitor. During a trial, a single image appeared in 24-bit color, enlarged to approximately life size, for 5 sec (i.e., animals viewed one image after another). The presentation time was kept to a minimum because longer trial durations can lead to animal boredom and inattention [Waitt, 2005]. The order of stimuli was randomized, and presentations of red or non-red versions of the stimuli were counterbalanced among subjects (i.e., animals viewed each face and hindquarter once, in either a red or non-red version, so that each animal saw four red faces, four red hindquarters, four non-red faces, and four non-red hindquarters), since viewing images more than once can lead to a marked reduction in interest [Wilson & Goldman-Rakic, 1994]. There were 16 trials in total.

A trial was excluded if the eye gaze was obscured (i.e., animals were oriented with their backs to the monitors or had their eyes closed for the entire trial). The mean number of trials included per animal was 14.58 (SE = .29). If an animal attended to less than 50% of trials within a session, the session was excluded from the analyses and a second attempt was conducted 5 days later. One male was retested and then later excluded from the analyses because he failed to meet the criteria during both testing sessions. The testing sessions lasted 2–7 min (mean = 3 min 40 sec, SD = 1 min 37 sec).

Observer software (Noldus, 3.0) was programmed to continuously record the study animals' visual gaze duration as a measure of attention, during frame-by-frame analyses, as well as all behavioral responses (i.e., lipsmacking, grimaces, approaches, and withdraws) to the images. The order of stimuli was unknown to the experimenter recording these data. To assess intraobserver reliability, sessions from two individuals were randomly selected, and original and reanalyzed scores were assessed. Scores for looking duration were compared in trial-by-trial correlations, yielding reliability coefficients of .90 and .92 [Martin & Bateson, 1993].

Two-tailed paired *t*-tests were employed to determine whether facial and hindquarter color influenced gaze duration and behavioral responses. A repeated-measures analysis of variance (ANOVA) was used to assess whether the order of trials influenced gaze duration, to gauge whether significant changes in attention occurred over testing sessions. All analyses had a significance level of $P < 0.05$ and were performed in SPSS 11.0.

RESULTS

Male gaze duration was not significantly influenced by female facial color ($t_{18} = .95$, $P = .356$), and only 10 of the 19 subjects had longer viewing times for red faces. However, males gazed significantly longer at images of red vs. non-red hindquarters ($t_{18} = -2.38$, $P = .029$). Thirteen males displayed longer gaze durations for red hindquarters (see Fig. 1). Behavioral responses toward images were infrequent and highly variable among individuals, and all were nonsignificant in relation to color. Trial number did not have a significant influence on attention ($F_{1,18} = 1.67$, $P = .213$), and the mean gaze durations in the first and last trials were very similar (2.45 sec, SE = .38 vs. 2.14 sec, SE = .42), suggesting that little habituation occurred over the experiment.

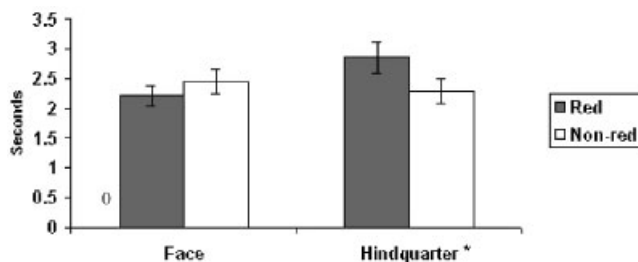


Fig. 1. Mean male gaze duration (in seconds) and SE per trial for red and non-red female faces and hindquarters (* $P < .05$).

DISCUSSION

This study suggests that male visual preferences are influenced by the color of the anogenital skin, but female facial color has no impact on male preferences, indicating that displays of red coloration alone are not sufficient to elicit attention from males. This finding contrasts with recent experimental data showing that females pay selective attention to differences in the facial color of other females (Gerald et al., unpublished results), indicating the existence of sex differences in attention to female facial color. In contrast to the previous study by Bielert and colleagues [1989], male behavioral reactions to females in the present study were infrequent and limited to occasional lipsmacking, grimaces, approaches, and withdraws, and none varied significantly in relation to color. This highlights one shortcoming of using such methods, and using live animals is more likely to produce more meaningful behavioral responses.

The current results also differ from the finding by Waitt et al. [2003] that female rhesus macaques pay selective attention to images of males with reddened faces. In rhesus macaques, female facial color may be less important to males compared to the coloration of anogenital sexual skins because the color of female facial sexual skin fluctuates little over the cycle [Baulu, 1976], and therefore appears to be a less reliable signal for pinpointing cyclical fertility.

The disparity between male and female attention directed to female facial color suggests that it may serve a purpose other than that of attracting males. Although male and female faces may overlap in coloration, this does not necessarily indicate that coloration has the same functional significance for both sexes [Gerald, 2003]. Red male facial sexual skin has been suggested to be an honest signal of condition, which may reflect individual competitive ability [Setchell & Wickings, 2005; Waitt et al., 2003], and wearing red has even been linked with successful competitive outcomes in human athletic events [Hill & Barton, 2005]. As such, this signal may be employed by females to assess mate quality [Waitt et al., 2003]. In female rhesus macaques, facial hue has been associated with rates of intrasexual affiliation, and facial color saturation has been inversely related to received aggression, suggesting that components of face color may play a role in regulating female–female interactions (Gerald et al., unpublished results). If female facial color is indicative of competitive ability, males may be less concerned with female signals of quality compared to signals of fertility. This would be consistent with Nunn's [1999] graded-signal hypothesis, which suggests that males are interested in female sexual skin to assess the probability of ovulation, rather than to assess female quality. Such results would also be consistent with research in other taxa suggesting that multiple

Attention to Female Secondary Sexual Color / 743

ornaments act to convey different messages to potential mates vs. competitors [e.g., Andersson et al., 2002]. We conclude that the signal function of sexual skin may vary across anatomical regions, and that such signals may be directed toward different groups of receivers. Future studies should examine male reactions to varying intensities of female color.

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