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Visual preferences for sex and status in female rhesus macaques

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Abstract

Most primates are both highly visual and highly social. These qualities predict that visual cues to social variables, such as identity, sex, social status, and reproductive quality, would be intrinsically valuable and systematically attract attention. Supporting this idea, thirsty male rhesus macaques (*Macaca mulatta*) will forego fluid reward to view images of the faces of high-ranking males and the sexual skin of females. Whether female rhesus macaques, who experience dramatically different social pressures and reproductive costs than male macaques, also systematically and spontaneously value visual cues to social information remains untested experimentally. We probed the preferences of female rhesus macaques, given the opportunity to display an image from a known class of social stimuli or touch a second target to display a blank screen. We found that females preferred faces of high-status males and also images of the perineum of both males and females, but were not motivated to display images of subordinate males or control stimuli. These findings endorse the view that both male and female rhesus macaques—and presumably other highly social primates—seek information about other individuals in a way that matches the adaptive value of that information for guiding social behavior.

Keywords

Macaca mulatta; Social; Dominant; Subordinate; Status; Hierarchy

Introduction

The evolution of complex social behavior in primates parallels the evolution of sensorineural specializations for binocular vision, enhanced visual processing, and selective

attention (Van Essen et al. 1992; Barton 1998; Allman 2000). The co-evolution of these traits suggests the hypothesis that there is adaptive value to acquiring visual information about conspecifics, including their identity, sex, status, and reproductive quality. Supporting this idea, humans (Johnson et al. 1991), rhesus macaques (Sugita 2008), chimpanzees (Hattori et al. 2010), and ringtail lemurs (Shepherd and Platt 2008) preferentially orient to the faces of conspecifics, and both male rhesus macaques (Andrews and Rosenblum 1993; Brannon et al. 2004) and humans (Aharon et al. 2001) (Hayden et al. 2007) will work to see other individuals. The intrinsic value of visual social information is further supported by the observation that photos of the faces of dominant males or the perinea of females substitute for fluid rewards for thirsty male rhesus macaques choosing between options rewarded with different amounts of fluid (Deaner et al. 2005; Klein et al. 2008). These findings endorse the notion that visual social stimuli have reinforcement value that varies with the content of the information displayed.

Many of these prior studies have been conducted on males (Andrews and Rosenblum 1993; Deaner et al. 2005; Klein et al. 2008; Shepherd and Platt 2008). The mechanisms that mediate dominance in the two sexes, however, are often different, suggesting possible differences in the adaptive value of visual social stimuli. In rhesus macaques, for example, female status is stable and linear, with daughters securing ranks similar to those of their mothers, whereas the ranks of males typically changes many times during their lives (Gachot-Neveu and Menard 2004). Moreover, females remain in the same social group for the duration of their lives, whereas males will typically emigrate from their natal group at adolescence (Gachot-Neveu and Menard 2004).

Active mate choice by females further suggests that information about mate quality may be valuable to them. Females experience high reproductive costs due to lactation, gestation, and maternal care, as evidenced by a peak in female, but not male, mortality during the birth season (Hoffman et al. 2008). Because the costs of carrying and raising offspring are much higher for females than for males, female macaques should be highly selective with regard to mate choice. It is well-known that macaques can use proximity maintenance and vocalizations to express mate choice for particular males and can reject mounting of unpreferred males (Soltis 2004). Female macaques prefer to mate with higher ranking males, either for their genetic quality (Sackett 1990; Hauser 1993) or to protect themselves or their offspring from aggression (Wrangham 1979; Smuts 1987).

Inherited social rank, philopatry, and status-guided mate choice in female rhesus macaques suggest that they may value particular classes of visual social information and that this valuation may not be identical to that of males (as in Deaner et al. 2005). Given female mating preferences for high-ranking males, we hypothesized that female rhesus macaques would seek visual information about dominant males and specifically predicted that they would find images of dominant male faces to be reinforcing. We additionally tested the hypothesis that female macaques would value the opportunity to acquire information about potential mate quality, and therefore predicted that female macaques would find male perinea reinforcing as well. To test our hypotheses, we used a visual preference task analogous to the one used previously with male rhesus macaques (Deaner et al. 2005; Klein et al. 2008) with unrestrained female rhesus macaques.

Methods

Four adult female rhesus macaques served as subjects. They were group-housed together in a gang of four cages (Primate Products, Inc., Immokalee, FL) and had auditory and visual contact with the rest of the colony, consisting of 10 male rhesus macaques in the same room. All testing was conducted in accordance with regulations governing the care and use of

laboratory animals and had prior approval from the Institutional Animal Care and Use Committee of Duke University.

Behavioral task

The behavioral task was based on the method of constant stimuli (Fechner 1966) and was modified from that used previously (Deaner et al. 2005) in order to accommodate unrestrained monkeys (Fig. 1a). In this method, choice rates are determined for various image classes relative to a neutral alternative (a blank screen). This allows the efficient calculation of the ordinal rank of a number of different image categories, as opposed to measuring choice rates directly by testing all possible pairwise image category comparisons.

All subjects performed the task while temporarily housed alone in one of the four gang cages, but were otherwise unrestrained (Fig. 1a). Stimulus presentation, data collection, and reward delivery were controlled by the Gramalkn Experiment Control System (ryklinsoftware.com) running on a Dell Dimension 8400 computer. Stimuli were displayed on a 15-inch touch-screen monitor (Elo Touch-Systems 1547L, Tyco Electronics, Menlo Park, California) at a resolution of $768 \times 1,024$ and a rate of 60 Hz, attached to the open door of the home cage.

Trials were initiated by a 300-ms broadband tone and the appearance of a 200×200 central fixation square (Fig. 1c). Subjects had 10 s to touch the square, which caused the central fixation cue to be replaced by two diametrically opposed targets: T1, a 200×200 green circle centered 15 visual degrees to the left of the monitor origin and T2, a 200×200 red circle centered 15 visual degrees to the right of the monitor origin. Selection of T1 via touch yielded a pellet reward and a blank screen, whereas selection of the T2 target via touch yielded a pellet reward and a 500-ms presentation of an image. The spatial location of the targets and the associated images were fixed for the duration of each session. Trials were considered error trials if the animal failed to touch the initial central square within 10 s of the trial initiation tone, or if a target was not selected within 5 s of onset. For each completed trial, the monkey received a sugar pellet reward (TestDiet Sucrose Tab/Banana 190 mg, Richmond, Indiana) delivered by an automated pellet dispenser (ENV-203-190IR, Med Associates, Inc., Georgia, Vermont). In the case of error, the trial was terminated without penalty to the animal, and a new trial was initiated. Intertrial interval was 2 s.

Sessions were always initiated with the completion of two “forced” trials for each target (T1 in absence of T2, or vice versa) presented in random order. These trials ensured that the monkeys were informed about the category of image that was to be associated with T2 on that session, as well as the location and target identity associated with each option (blank vs. image). After the successful completion of two T1 forced trials and two T2 forced trials, free choice trials with both targets present commenced. Only completed choice trials were used for analysis.

Sessions were terminated when the subject ceased participation in the experiment (as marked by >15 consecutive error trials), when the subject had completed at least 30 choice trials, or if the experiment was interrupted by external events such as husbandry activities. Only sessions with at least 10 valid choice trials were included in the analysis. Choice frequency was calculated for the entire session, such that each session contributed a single data point. Typically, only a single image category was presented each session.

Visual stimuli database and display

Digital photographs of conspecifics elicit species-typical responses from Old World monkeys such as macaques, supporting the use of such stimuli to probe social cognition experimentally (Deaner and Platt 2003; Waite and Buchanan-Smith 2006). In our

experiment, social image stimuli consisted of color bitmaps ranging in size from 115×115 to 130×130 pixels displayed on a $1,024 \times 768$ monitor at a 60 Hz refresh rate (Fig. 1c). Using Matlab, images were adjusted to match their overall luminance to the luminance of the gray square. Additionally, we calculated, as a percentage, the contribution of the red channel relative to the other channels in each RGB image.

Images were drawn randomly with replacement from one of the following four image pools: High-status male, low-status male, female perinea, male perinea, or gray square (Fig. 1b). All image pools except the gray square consisted of 60 images. Both high-status and low-status male pools consisted of 20 face images of 3 different individuals (60 images per pool) whose social status remained stable over the duration of the experiment (see “Assessment of Male Dominance Status” below). All individuals depicted in the images were housed in the same room and had auditory and visual contact with the female subjects. Therefore, the social statuses of all the individuals depicted in the image pools were known to the subjects. The male perinea and female perinea pools consisted of 15 images from 4 different individuals each (60 images total). The gray square image pool consisted of a single 292×292 image. Previous studies indicate that choice-based preferences for images within the size range used here are not affected by image size (Deaner et al. 2005).

To create the stimuli, photographs of monkey faces were collected using a digital camera, while the monkeys were seated comfortably in a primate chair with head restrained (Deaner et al. 2005). Images were selected for neutral expression and were approximately balanced for direct and averted gaze direction. Both eyes were visible in each image. Perinea images were collected while the animal was standing on the floor of the colony room with all four feet on the floor. During photography sessions, the animal was lightly restrained via pole-and-collar in a manner that allowed some movement, but prevented agonistic interactions with the other animals in the colony room. Monkeys were not engaged in active behavioral display at the time of image collection.

Assessment of male dominance status

We used a controlled confrontation method (described also in Deaner et al. 2005) to assess the social dominance of the monkeys used to generate stimuli. While seated in covered primate chairs, two monkeys were brought into a familiar environment out of visual contact from the rest of the colony. The chairs were placed directly facing each other and covers were removed. The monkeys' heads were approximately 45 cm apart, and these positions were maintained for approximately 2 min. A digital camera was placed on a tripod approximately 3 m. from the monkeys. To estimate the percentage of time that monkeys looked toward each other, we used point sampling with 1-s intervals (Altmann 1974). For the first 60 samples, we scored the subjects as looking directly toward the other monkey or not (based on head position). In addition, all male monkeys were pair-housed, and each monkey represented in the high-status category was higher status than his cage mate as well as each of the monkeys in the low-status category. Similarly, each monkey in the low-status category was lower status than his cage mate as well as each of the three monkeys in the high-status category. Dominance assessments determined in this manner matched experimenter observations of each pair in their home cages.

Data analysis

Statistics were performed using Statistica (Statsoft, Tulsa, OK). Image choice rate, the percentage of trials in a session for which the monkey chose the image over the blank, was determined for each session. Choice data from each subject were confirmed to be from a normal distribution (Lillifors test; $P > 0.06$ for all) and of equal variance (Bartlett's statistic 1.81, $df = 3$, $P = 0.61$). Based on this, parametric statistical methods were applied.

Results

111 behavioral sessions were collected from four female rhesus macaques (see Table 1). Monkeys picked the image target most frequently when it predicted the display of a female perineum ($59.0 \pm 6.7\%$ mean $\pm$ S.E.) or male perineum ($54.2 \pm 9.0\%$), less frequently when the image was of a high-status male face ($43.6 \pm 0.10\%$) or low-status male face (40.0 ± 0.08), and least of all when it was a gray square ($28.7 \pm 0.06\%$; Fig. 2a, b). We used an ANCOVA to assess whether the category of image significantly influenced image choice rates. In order to control for the effect of having multiple sessions, we included “subject” as a categorical predictor and “session number” as a continuous predictor. Both subject ($F(3,73) = 70.0$, $P < 0.0001$) and image category ($F(4,73) = 4.73$, $P < 0.0001$) had significant effects on choice behavior, indicating systematic preferences for particular image pools across all monkeys, as well as individual differences in overall rates of responding. However, session number had no significant effect on choice rates ($F(1,73) = 2.55$, $P > 0.11$).

In order to determine which image categories induced higher rates of responding than the gray square, we used the Dunnett test. We found that the high-status male faces and both male and female perineae had significantly higher choice rates than the non-social gray square control image (all $P < 0.0001$). By contrast, the low-status male faces were not chosen more frequently than the gray square ($P > 0.20$).

We next sought to determine whether the identities of the individual monkeys depicted in each face image pool influenced choice rates. To do this, we restricted our analysis to those trials that displayed a face image and performed a logistic regression on the subsequent trial's outcome (choice of image or blank). Subject name, image category, and the identity of the depicted monkey were included as regressors. Although subject and image category had a significant influence on choice (Wald's statistic 27.5, $P < 0.0001$ and Wald's statistic 4.78, $P < 0.03$, respectively), the specific identity of the monkey in the image did not (Wald's statistic 1.52, $P > 0.20$).

Previous reports indicate that the redness of a social image can influence visual preferences in female rhesus macaques (Waite et al. 2003). To examine whether redness influenced image choice in the females in our study, we tested whether an image's redness level influenced choice in the next trial. Restricting our analysis to trials that displayed a social image (i.e., excluding gray square sessions and trials for which the monkey chose the blank), we performed a logistic regression on the subsequent trial outcome using subject name, image category, and the image redness level (the mean value of the red channel in each luminosity balanced RGB image, as measured in Matlab), as regressors. These results indicated that the level of red in the image had no influence on choice rates ($P > 0.96$ for redness; $P < 0.001$ for all other factors).

Discussion

Like male rhesus macaques, female rhesus macaques valued specific classes of visual images of other rhesus macaques. As predicted, females found faces of dominant males and the perineae of males and females to be more reinforcing than a non-social control stimulus. These results are consistent with the hypothesis that there is reinforcement value to acquiring visual information about conspecifics.

One explanation for the observation that females showed a preference for dominant male faces, but not for subordinate male faces, is that females prefer high-status males as potential mates, and therefore seek to gather information relevant to reproductive quality. Consistent with this explanation, male position in the dominance hierarchy correlates with breeding

activity in macaques (Kaufmann 1965; Smith 1981). Sexually mature male macaques exhibit increased reddening of the skin in the face and perianal regions during the mating season due to vascular engorgement, and the intensity of color change correlates with fluctuations in plasma testosterone (Baulu 1976). Female macaques are known to visually attend to reddened over non-reddened male faces (Waite et al. 2003) and symmetric over non-symmetric faces (Waite and Little 2006), both potential signals of male quality.

A complementary explanation is that female macaques attend to dominant males, but not subordinate males, due to increased vigilance to potential threats. Preferences for viewing dominant male faces are modulated by serotonin transporter genotype in males, possibly through influences on sensitivity to social threats and social anxiety (Hariri and Holmes 2006; Watson et al. 2009). High-ranking males are more likely to initiate and win aggressive encounters than other members of the troop (Chapais 1983; Chapais 1986), and females can incur considerable costs due to male aggression, which can be fatal (Lindburg 1983; Chapais 1986; Manson 1992, 1994). Furthermore, dominant males are known to disrupt females mating with other males (Deelvira and Herndon 1986) and to use aggression to prevent females from forming or maintaining consortships with low-ranking males (Manson 1994). Heightened vigilance by females in the presence of potentially aggressive males has been observed in field studies of many primate species (Busse 1984; Fairbanks and McGuire 1987).

In comparison to the other image categories, the gray square elicited lower approach responses from females and was chosen at a frequency similar to that of the low-status male faces. We point out that the absolute choice rates of the image do not reflect the overall valuation of a particular image category (choice frequency different from 50% cannot be disambiguated from side bias in our subjects). Nevertheless, the gray square elicited the lowest rates of image choice for all four individual subjects, strongly suggesting that, in relative terms, the gray square had negative reinforcement value. This apparent aversion to a so-called neutral stimulus may reflect “range adaptation,” in which an outcome is valued in terms of the other possible outcomes available in a given context. In this sense, the gray square takes on negative reinforcement value because its appearance indicates an absence of potentially rewarding social information. This interpretation is consistent with recent findings showing that responses of reward-related neurons in the rhesus macaque brain are modulated by the value of alternative outcomes (Padoa-Schioppa 2009; Kobayashi et al. 2010).

The female subjects in our study chose to view male perineal areas at a significantly higher frequency than the gray square images, suggesting that male perineal areas have reinforcement value. Because females have such high reproductive costs, they must be highly selective when choosing potential mates. Thus, we expected our females to be predisposed to value the opportunity to gather information about male quality. In other primates, colored patches are thought to function as advertisements for male quality (Bergman et al. 2009), and the vividness of these patches are correlated with the number of approaches and sexual presentations males receive from females (e.g., in mandrills, Setchell 2005). Our monkeys were shielded from seasonal cues and mating opportunities, which precluded any “mating season.” We note, however, that male macaques play an important role in resource defense and protection from predators outside of mating season, and the ability of male macaques to fulfill these roles is strongly related to desirability as a mate. For these reasons, we speculate that females continually assess morphological indicators of health, aggression, and testosterone levels.

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Fig. 1.

Experimental design. **a** Rhesus macaques interacted with the experimental apparatus in their home cages. A touch-screen monitor was mounted flush with the wall of the cage. Each successfully completed trial was rewarded with a sugar pellet. **b** Time course of each trial. Trials were initiated with the onset of a short (300 ms) tone and the presentation of central square. Touching the square caused two touch-screen targets to appear, denoted here as T1 and T2. Touching T1 resulted in a blank screen and a fruit pellet, whereas touching T2 resulted in an image presentation and a fruit pellet. **c** Example images used in the experiment. *Top left* female perineia; *top right* male perineia; *bottom left* high-status male face; *bottom right* low-status male face. Each category except for the *gray square* (not shown) contained 60 different images. The *gray square category* consisted of a single image

Fig. 2. Female rhesus macaques preferentially value distinct classes of social information. Mean choice values for the various image categories, calculated across sessions. *Error bars* indicate SEM *indicates $P < 0.01$ in comparison to the *gray square*

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Table 1

Number of sessions run for each image category for each subject

	Gray	Low	High	Male peri	Female peri
Monkey B	4	6	7	8	5
Monkey S	3	3	4	10	4
Monkey F	3	6	8	7	8
Monkey M	3	5	7	6	4

Gray = gray square, low = low-status faces, high = high-status faces, male peri = male perineu, female peri = female perineu