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Monkeys Pay Per View: Adaptive Valuation of Social Images by Rhesus Macaques

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Summary

Individuals value information that improves decision making. When social interactions complicate the decision process, acquiring information about others should be particularly valuable [1]. In primate societies, kinship, dominance, and reproductive status regulate social interactions [2, 3] and should therefore systematically influence the value of social information, but this has never been demonstrated. Here, we show that monkeys differentially value the opportunity to acquire visual information about particular classes of social images. Male rhesus macaques sacrificed fluid for the opportunity to view female perinea and the faces of high-status monkeys but required fluid overpayment to view the faces of low-status monkeys. Social value was highly consistent across subjects, independent of particular images displayed, and only partially predictive of how long subjects chose to view each image. These data demonstrate that visual orienting decisions reflect the specific social content of visual information and provide the first experimental evidence that monkeys spontaneously discriminate images of others based on social status.

Results and Discussion

Most primates live in complex societies where the cultivation and exploitation of social relationships is associated with enhanced fitness [4–6]. Furthermore, across primate species, the size of the neocortex, the part of the brain devoted to higher-order information processing, scales with group size [7, 8]. These observations support the long-standing hypothesis that acquiring, storing, and using social information has been a potent selective force in the evolution of primate cognition [3, 9, 10].

The importance of acquiring social information is suggested by studies demonstrating that primates find social stimuli rewarding [11]. For example, primates will perform a variety of behaviors, including pressing levers [12] or moving their heads into a viewing channel [13], to gain visual access to other individuals. Moreover, primates will sometimes forego food rewards to view videos of other individuals [14]. These studies, and others like them, imply that the primate brain is predisposed to acquire social information [3, 10].

An evolutionary perspective on social cognition, however, makes the stronger prediction that primates should selectively acquire information about others that is most useful for guiding behavior. In most primate societies, behavior is structured by kinship, dominance, and reproductive status [2, 3], suggesting that social information should be valued according to these attributes [15]. Specifically, male primates should be willing to pay for information about powerful males or sexually receptive females because these individuals most strongly influence their own behavior [16, 17] and eventual reproductive success [5, 6]. In contrast, they should be less willing to pay for information about low-status individuals because they are less influential.

We tested this hypothesis by developing a new technique that asked monkeys to evaluate different visual images with a common fluid currency, thus permitting us to directly compare the subjective valuation of different classes of social information. In this paradigm, male rhesus macaques performed a choice task pitting fluid rewards against brief pulses of visual information (Figure 1A). On each trial, a monkey was permitted to shift gaze to one of two targets; orienting to target 1 (T1) yielded fruit juice, whereas orienting to target 2 (T2) yielded juice and the appearance of an image. Gaze was measured by the scleral search coil technique [18].

All monkeys in our colony room were housed in pairs or small groups with stable, unidirectional dominance relationships [19] and were also in visual and auditory contact with all other individuals. For purposes of colony management, not all monkeys had the opportunity to interact physically with each other, so we did not attempt to infer a linear dominance hierarchy across all animals. However, we were able to confirm that rank relationships within pairs generalized across monkeys within the colony. When males from different pairs were introduced to each other in a controlled confrontation paradigm (see Experimental Procedures), low-status monkeys averted gaze from high-status monkeys, whereas high-status monkeys tended to look directly at low-status monkeys (mean % looking, high status = 30; low status = 5; all 12 dyads in same direction, binomial probability < 0.001). In most primate societies, including those of rhesus macaques, direct staring is a threatening gesture, whereas gaze aversion generally indicates anxiety and submissiveness [20, 21]. The consistent directionality of this behavior indicates that social status generalized across monkeys in the colony.

We constructed pools of images of each monkey to determine whether subjects differentially valued the opportunity to view different classes of individuals based on social status or reproductive potential, as predicted. In the first experiment, there were twelve face image pools, each consisting of roughly twenty pictures of a particular familiar monkey; eight of the familiar monkeys were male and four were female; four of these

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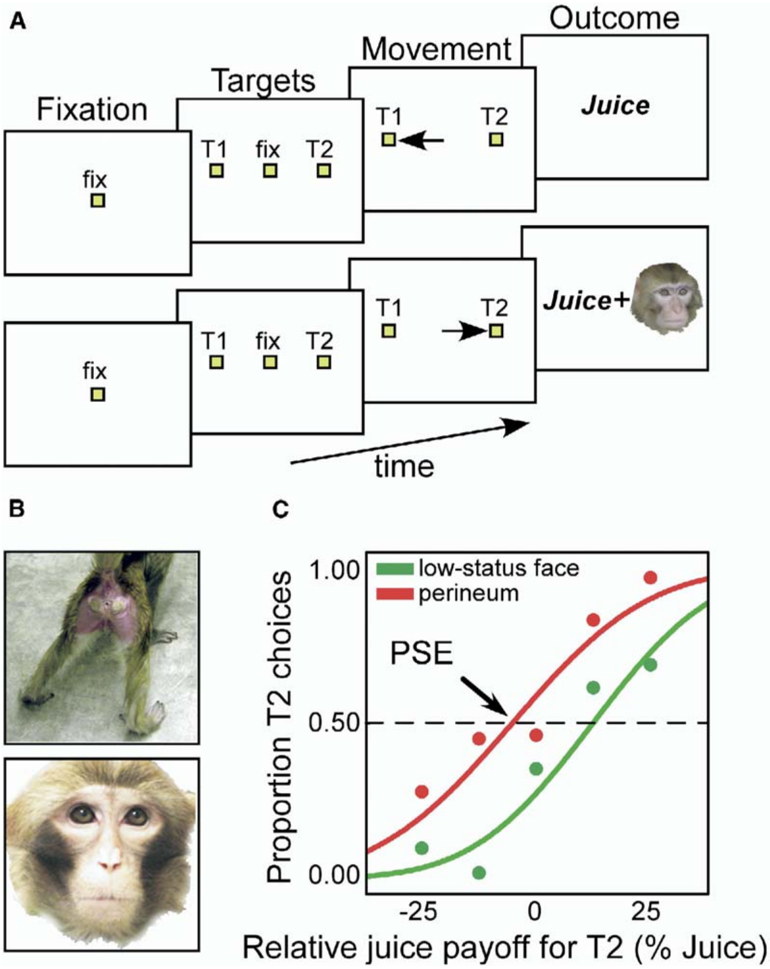

Figure 1. Task and Analysis for Estimating Image Valuation

(A) Behavioral task. Monkeys sat in a primate chair and fixated (± 1°–4°) a central yellow square (300–450 ms); then two yellow squares (T1 and T2) appeared 10°–20° peripherally, diametrically opposite the fixation square. Subjects maintained fixation (monkey M2, 100–130 ms; other monkeys, 250–300 ms); the fixation square then turned off, cuing subjects to shift gaze (<350 ms) to either target (± 3°–5°). Fixation ($\geq$500 ms) of target T1 resulted in juice; fixation ($\geq$500 ms) of T2 simultaneously yielded juice and an image at T2 (M2, 855–895 ms; other subjects, 630–670 ms). Subjects were then free to view images or to look away from them.

(B) Example images from a perineum pool and a low-status face pool.

(C) Method of PSE estimation, shown for a perineum pool block and low-status face pool block. PSE indicates the point of subjective equality (mean of cumulative normal function) where the subject was equally likely to orient to T1 and T2.

males and one of these females were of high-status; the others were of low-status. There were also two perineum image pools, each consisting of fifteen images of the hindquarters of the four familiar female monkeys. A gray square was also used as an image pool and served as a control (Figure 1B).

By varying across blocks of trials the amount of juice delivered for T1 and T2 choices, and the pool of images available for T2 choices, we were able to estimate the value, in fluid units, of orienting to view particular image pools (Figure 1C). We computed the orienting value for a given image pool on a given day based on the point of subjective equality (PSE), the amount of juice sacrificed or gained when a subject was equally likely to choose T1 and T2 (Figure 1C). Because we controlled our monkey subjects' access to fluid outside of experimental sessions, juice represented a biologically meaningful currency for estimating orienting value.

We predicted that male macaques would differentially value visual information according to its specific social content. In fact, both monkey subjects differentially valued social image pools (Figure 2A, left). Moreover, their valuations of all image pools, as well as face pools only, were highly correlated (Figure 2B; Spearman rank correlation: $n = 15$, $r_s = 0.82$, $p < 0.001$; faces: $n = 12$, $r_s = 0.78$, $p < 0.01$). The value monkeys placed on the opportunity to view particular image pools reflected their apparent importance for guiding social behavior. Despite being thirsty, both monkey subjects sacrificed juice to view female perinea and the faces of high-status monkeys but required fluid payment to view the faces of low-status monkeys (Figure 3A, left). Ranked orienting values confirmed these results: both subjects valued low-status faces less than either high-status faces (Mann-Whitney: monkey M7: $z = 2.52$, $p < 0.05$; monkey M2: $z = 2.35$, $p < 0.05$) or perinea (M7: $z = 2.05$, $p < 0.05$; M2: $z = 2.05$, $p < 0.05$). Consistent with some prior studies [14, 22], neither monkey showed an overall tendency to value social images more than the control image (M7: $t(109) = 0.60$, $p = 0.54$; M2: $t(83) = 0.83$, $p = 0.74$). Instead, orienting value reflected the specific social content of images.

Because four out of five high-status monkeys in our stimulus set were male, the greater valuation of high-status faces could reflect a greater valuation of males compared to females rather than an effect of social status. To address this issue, we analyzed the orienting value of male faces alone. Orienting values of high-status male faces were significantly greater than those of low-status male faces ($F_{1,72} = 4.06$, $p < 0.05$), and

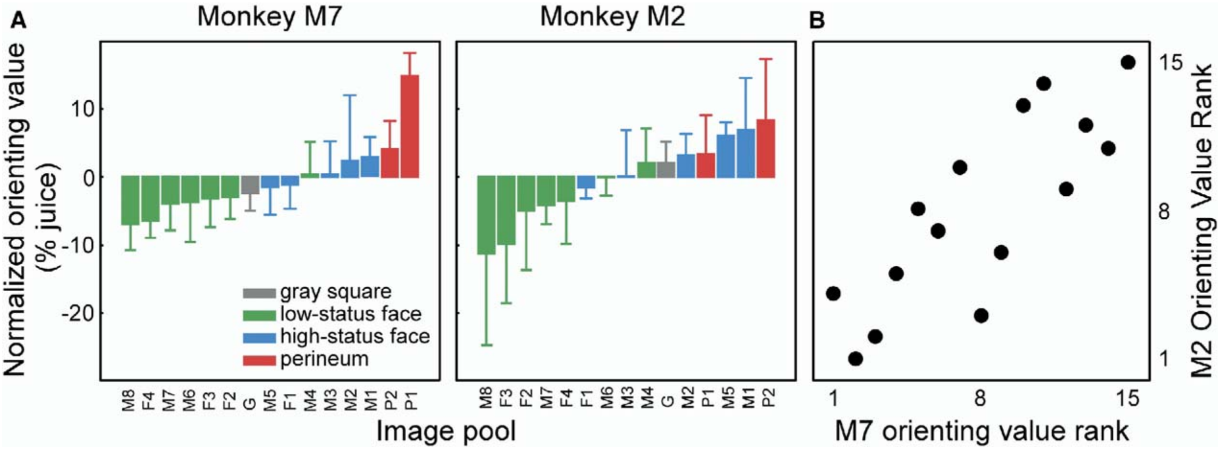

Figure 2. Monkeys Differentially Value Image Pools and Their Valuations Are Correlated

(A) Mean normalized orienting values (±SEM) for M7 and M2 for pools of gray squares, low-status faces, high-status faces, and female perinea. Orienting values are sign-reversed PSEs (Figure 1C).

(B) M7's orienting value rank plotted against M2's orienting value rank.

orienting value ranks showed the same difference (M7: $z = 2.02$, $p < 0.05$; M2: $z = 2.02$, $p < 0.05$). Furthermore, monkeys did not value low-status male faces more than low-status female faces ($F_{1,75} = 0.23$, $p = 0.63$; ranks, M7: $z = 0.35$, $p = 0.73$; M2: $z = 0.71$, $p = 0.48$). Face value was, thus, a specific function of social status and not gender.

To test the robustness of our findings, we repeated this experiment with the gray square and five novel image pools: one pool each of two familiar high-status male faces, one pool each of two familiar low-status male faces, and one pool of four familiar females' perinea. One monkey from the initial experiment (M7) and two additional male monkeys (M6 and M3) served as subjects. As in the first experiment, monkeys paid for the opportunity to view female perinea and the faces of high-status monkeys but required fluid payment to view the faces of low-status monkeys (Figure 3A, right). The small number of image pools precluded within-subjects tests, but for all three subjects, median orienting value ranks were lower for both high-status faces and perinea than for low-status faces or gray squares. Thus, differential valuation of visual information by social content was demonstrated for four monkeys and with two completely different sets of images. Moreover, all monkeys showed the same patterns of valuation despite differing in social status (M2 and M3 were high-status; M7 and M6 were low-status).

The differential valuation of social images was psychologically and physiologically meaningful for our subjects. Because we controlled their access to fluid outside of experimental sessions, all four monkeys were very sensitive to small differences in the amount of juice delivered for choosing each target [23]. To estimate this sensitivity, we used the standard deviations (SD) of cumulative normal functions fit to the raw choice data during blocks with the gray square (mean SD = 19%). Our monkeys valued perinea and high-status faces about 10% more than low-status faces, relative to the average fluid value of the two targets. Based on our sensitivity analysis, these same monkeys would detect an equivalent difference in actual juice value (~½ SD) about 70% of the time in blocks with the nonsocial control image. Therefore, the amount of juice our monkeys paid to view female perinea and the faces of high-status monkeys was well within their fluid discrimination capacity and, thus, represented a genuine reversal of their usual preference for more juice.

Another potential measure of value is the duration or frequency with which an individual looks at a stimulus [3, 24]. In the choice task, stimuli were displayed briefly, but subjects nonetheless looked longer at particular classes of images (Figure 3B). In both experiments, all subjects' viewing times were longest for perinea, intermediate for faces, and shortest for the gray square. However, no subject's viewing times discriminated between low-status and high-status faces. These analyses suggest that orienting value and viewing time index different aspects of social utility.

An important question is whether orienting value or viewing time reflected motivation to view images with particular visual characteristics, such as high luminance, contrast, size, or redness [25]. None of these properties predicted either orienting value or viewing time for any subject in either experiment (Spearman rank correlations, $p > 0.05$ in all 40 cases). For experiment 1, we also scored each of the face image pools for the number of images with face oriented forward, eyes oriented forward, or nonneutral expression [12]. None of these features predicted orienting value or viewing time for either monkey ($p > 0.05$ in all 12 cases). For experiment 2, face pools were constructed to be invariant in these characteristics. In this task, therefore, neither orienting value nor viewing time can be explained in terms of low-level stimulus features, facial expression, or gaze orientation.

Another notable aspect of our study is that subjects tended to evaluate images of their own faces according to their status (Figure 2A; high-status self faces versus high-status other faces, experiment 1, M2: $F_{1,24} = 0.01$, $p = 0.93$; experiment 2, M3: $F_{1,1} = 6.43$, $p = 0.24$; low-status self faces versus low-status other faces, exp. 1,

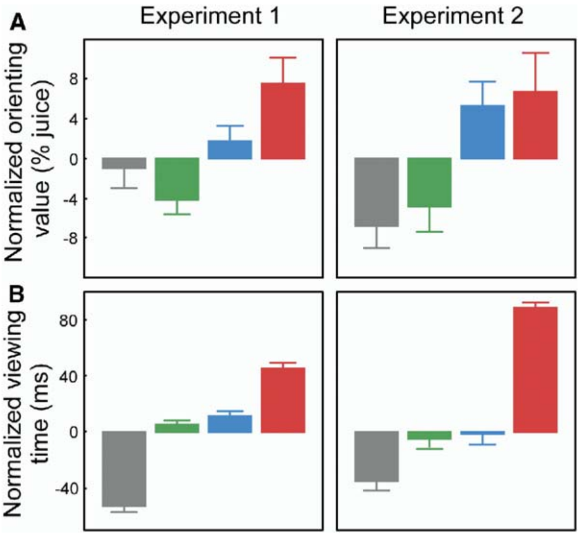

Figure. 3. Male Monkeys Sacrifice Fluid to View Female Perinea and High-Status Faces but Require Fluid Payment to View Low-Status Faces; Once Chosen, Time Spent Viewing Faces Does Not Differ According to Social Status

(A) Mean normalized orienting values (±SEM) varied across image classes (experiment 1: $F_{3,188} = 6.12$, $p < 0.001$; experiment 2: $F_{3,41} = 5.99$, $p < 0.01$; no significant main effect of subject or interaction between subject and image class for either experiment). High-status faces were more highly valued than low-status faces (post-hoc Tukey hsd: both experiments $p < 0.05$) and the gray square (experiment 2, $p < 0.05$); perinea were more valued than low-status faces (experiment 1, $p < 0.001$; experiment 2, $p < 0.05$) and the gray square (both experiments, $p < 0.05$).

(B) Mean normalized viewing times (±SEM) varied across image classes (experiment 1: $F_{3,8574} = 102.41$, $p < 0.001$; experiment 2: $F_{3,2261} = 44.71$, $p < 0.001$). Because there was a main effect of subject in experiment 2 ($F_{2,2261} = 3.74$, $p < 0.05$) and interactions between subject and image class in both experiments (experiment 1: $F_{3,8574} = 21.54$, $p < 0.001$; experiment 2: $F_{6,2261} = 3.56$, $p < 0.01$), we conducted post-hoc tests separately for each subject. All monkeys in both experiments viewed perinea longer than either the gray square (all, $p < 0.001$) or low ranking faces (M2: experiment 1, $p < 0.01$; experiment 2, $p < 0.05$; all others, $p < 0.001$). In experiment 2, two monkeys viewed perinea longer than high-status faces (M7, $p < 0.001$; M6, $p < 0.001$), and one monkey viewed high-status faces longer than the gray square (M7, $p < 0.05$).

M7: $F_{1,42} = 0.00$, $p = 0.99$; experiment 2, M7: $F_{1,1} = 2.05$, $p = 0.39$). Although this finding is consistent with a hypothesis of visual self-awareness [22], other explanations seem more likely. First, some facial features may covary with other physical factors associated with social status, and our monkeys may have responded to these features. Second, subjects had access to mirrors in their home cages and could thus have learned to associate their own face with threatening or submissive expressions associated with high or low status [26]. To investigate this possibility, we placed a full-length mirror in front of each of our 8 male monkeys while they were seated in a primate chair. All four high-status males threatened their mirror image. None of the low-status monkeys did so, and one of them (M6) gave unambiguous submissive displays. Moreover, high-status monkeys spent 41% of the mirror session looking directly at their reflection, whereas low-status monkeys did so for only 19% of the session (Mann-Whitney on ranked % looking: $z = 2.02$, $p < 0.05$). Thus, high-status monkeys may have had greater reason to respond to images of their own faces as if they were high-status monkeys.

Our data demonstrate that monkeys value visual information according to its apparent utility for guiding adaptive social behavior in the wild. The high value placed by males on visual access to female genitalia is consistent with the observation that swollen perinea evoke profound behavioral changes in males in the wild, including visual inspections, mating attempts, and increased male-male competition [27]. Intriguingly, our male subjects generally did not value the opportunity to view female faces over male faces. This suggests that the high value of viewing perinea did not reflect a nonspecific drive for access to females in general but was specific to the information contained in the images.

Our results also provide the first experimental evidence that monkeys spontaneously discriminate images of other individuals based on social status [28]. Such discrimination is likely based on knowledge of social relationships. A second, compatible possibility mentioned above is that some facial features predict social status and our monkeys responded to these features. Humans apparently make judgements of rank by using facial cues [26, 29] as well as social knowledge. Further research is necessary to determine the relative contribution of social knowledge and facial cues to status discrimination in monkeys.

Wild male macaques closely monitor the status and fighting ability of males in other groups [17], and both male and female primates appear to look more frequently at high-status animals [30–32]. Our results indicate that primates engage in such monitoring because it yields social information of measurable value. Our data also suggest that monkeys choose whom to look at, at least in part, based on social status, a prediction of the long-standing hypothesis that primate social structure is reinforced by allocating attention according to social rank [15]. The close correspondence between our monkeys' valuation of social information and its apparent utility for natural behavior is all the more striking because our subjects were housed in a captive colony with limited opportunity for physical contact except between pairmates.

Our results also indicate that viewing time and orienting value reflect different aspects of social utility. Orienting value measures a subject's willingness to sacrifice fluid, a physiologically necessary commodity, for the opportunity to gain visual information. Although direct viewing yields information, it may also impose distinct costs. Specifically, viewing both perinea and faces is likely to be highly informative, but prolonged staring at a face may be aversive because direct staring is a threatening gesture for rhesus macaques [20, 21]. Monkeys may therefore be predisposed to limit direct eye contact with others except when vital to the success of an aggressive encounter. Our data suggest that viewing time may index the composite value of orienting as a means to acquire social information and as a social signal, at least for faces. This implies that the neural computations governing where to look and for how long are distinct.

Finally, neurophysiological studies indicate that fluid value associated with visual targets systematically modulates neuronal activity in circuits governing visual orienting [33, 34]. Our data implies that these circuits must also have access to the value of social information. This system may be part of a suite of enhanced cognitive abilities and specialized neural machinery that evolved in the primate clade to solve social information processing problems associated with living in complex groups [3, 9, 10].

Experimental Procedures

Subjects and Housing

Four adult males from a colony of twelve rhesus macaques (*Macaca mulatta*) served as subjects. Eight males were pair housed and four females were cohoused; each was designated as high-status or low-status relative to its cagemate(s) based on unidirectional submissive displays [19]. High-status males remained dominant throughout the study (May 2003 to August 2004), whereas one female remained dominant to the other three females, whose rank relations were fluid. The cage positions and social groupings of all rhesus macaques were unchanged for more than one year prior to the initiation of the study. All animals were originally reared in social groups. Subjects were on controlled access to fluid outside of experimental sessions; they earned roughly 80% of their total daily fluid ration during experimental sessions. All procedures were approved by the Duke University Medical Center Institutional Animal Care and Use Committee and complied with the Public Health Service's Guide for the Care and Use of Animals.

Procedures

A Dell Precision 220 Pentium 4 computer controlled experiments and recorded data with custom software (http://ryklinsoftware.com/). Monkeys viewed stimuli with their eyes 45 cm from a 24 in Sony Trinitron monitor (1024 × 768 resolution; 60 Hz refresh). All stimuli were presented on a dark background. Eye position was monitored at 500 Hz with a scleral search coil [18] implanted with standard techniques described previously [35].

A solenoid controlled the duration of juice delivery, which varied randomly without replacement among five pairs of values (e.g., 130 ms/170 ms, 140 ms/160 ms, 150 ms/150 ms, 160 ms/140 ms, 170 ms/130 ms). Juice values varied every 30 trials; image pools varied every 150 trials. Spatial locations of T1 and T2 each varied from −20° to 20° horizontally and −15° to 15° vertically across sessions but always remained constant for each monkey on each day. Single target trials (20%–40% of all trials) were used to encourage subjects to sample both targets because neither juice nor image outcomes were cued. Single target trials were identical to choice trials in terms of timing, the receipt of juice rewards, and image outcomes.

In experiment 1, subjects completed roughly five (mean = 5.11) image pool blocks per session; in experiment 2 subjects completed six or seven image pool blocks per session. In experiment 1, monkeys completed 20 (M2) or 25 (M7) sessions; in experiment 2, monkeys completed three (M3) or four (M7 and M6) sessions. In experiment 1, in most sessions (92%), the gray square was tested first; other pools were tested pseudorandomly; the two perineum pools (10% each of all nongray pools) and the four female face pools (9% each of all nongray pools) were shown more frequently than the eight male face pools (6% each of all nongray pools) because of the greater number of males. In experiment 2, the gray square was always tested first; the five social pools were then tested randomly without replacement; in two of the 11 sessions, the gray square was retested after the social pools.

Stimuli

Images were produced from 2.1 megapixel digital photos (Sony Mavica MVC-CD1000). In experiment 1, approximately 20 (mean = 19.91; SD = 0.67) pictures composed each face image pool. Mean luminance was adjusted to match the gray square, the head was cropped from the background, and the image was resized to 115 × 115 pixels (width 5°). Two perineum pools (P1, P2) each consisted of 15 images from all four females. Photos of female perinea were taken on 3–4 days equally spaced over one month. Visual inspection indicated that all females were reproductively cycling during the photographic period and the study period. Perineum images were normalized in the same manner as face images except for background cropping.

For experiment 2, the high-status face pools were comprised of images from monkeys M2 and M3; the low-status face pools were comprised of images from M7 and M5. The stimuli in experiment 2 were created with the same techniques as in experiment 1. However, exactly 20 pictures composed each face and perineum pool, and faces were not cropped from the background. In addition, in experiment 2, all images in a pool were either 115 × 115 pixels or 230 × 230 pixels (width 10°). Large and small versions of image pools were alternated and counterbalanced across days so that subjects viewed similar numbers of large and small pools each day and so that each particular image pool was viewed roughly equally often in large and small versions. Normalized orienting values were unaffected by image size ($F_{1,45} = 2.27$, $p = 0.13$); thus, normalized orienting values derived from both large and small images were combined in the analyses presented in the Results and Discussion. Normalized viewing times (normalized relative to large and small images combined) were significantly longer for the larger images ($F_{1,3805} = 4.61$, $p < 0.05$). Therefore, we conducted viewing time analyses for large and small images separately (after normalizing them separately). For congruence with experiment 1, only analyses of small images are presented in the Results and Discussion and Figure 3B. For large images also, however, viewing times varied across image classes ($F_{3,1529} = 17.59$, $p < 0.001$). There was a main effect of subject ($F_{1,1529} = 8.56$, $p < 0.01$) and a subject by image class interaction ($F_{5,1529} = 6.47$, $p < 0.001$). Post hoc tests conducted separately on each subject revealed that one monkey (M7) viewed high-ranking faces and perinea longer than the gray square (both $p < 0.001$), and one monkey (M6) viewed perinea longer than high-status and low-status faces (both $p < 0.001$). No monkey differentially viewed high-status and low-status faces.

Analysis

Image characteristics were analyzed in Matlab. For experiment 1, face images were characterized as head forward (58)/averted (182), eyes forward (41)/averted (199), and expressive/vocalizing (31)/neutral (209). Interobserver reliability (R.O.D., A.V.K.) for image scoring was excellent (Cohen's $\kappa = 0.88, 0.84, 0.84$).

PSEs for each image block were derived from cumulative normal fits of the relative juice payoff for T2 choices plotted against the percentage of choice trials orienting to T2. These fits were calculated in Statistica 6.1 (StatSoft, Tulsa, OK) by the Hook-Jeeves and quasi-Newton estimation method; starting values were set at 0, initial step was set at 1, and the PSE estimates were constrained to values between −40 and 40. PSEs were highly correlated with the overall percentage of choice trials orienting to T2 (experiment 1: $r = -0.86$, $n = 194$, $p < 0.001$; experiment 2: $r = -0.84$, $n = 51$, $p < 0.001$).

Viewing time was measured from image onset until the first saccade > 7° (Eyemove software). If no saccade occurred during image display, viewing time was set to the maximum possible display time. Because satiety and the spatial positions of T1 and T2 varied across sessions, we normalized PSEs and viewing times. PSEs were normalized by subtracting the mean PSE of all image blocks in a session from PSE calculated for each image block in that session. Viewing time was normalized by subtracting the mean viewing time of all trials in a session from viewing time on each trial in that session. We also repeated the orienting value and viewing time analyses with the gray square for normalization and found highly similar results. Only image blocks with error rates less than 25% were included in analysis (experiment 1, 81%; experiment 2, 93%). Errors were defined as monkeys failing to correctly shift gaze from fixation (< 350 ms) to a target and maintain fixation for 500 ms. On error trials, subjects received no juice, and no image was displayed.

Controlled Confrontation Experiment

While seated in covered chairs (Crist Instruments, Hagerstown, MD), two monkeys were brought into a familiar experimental room.

Their chairs were placed directly facing each other, and the covers were removed. The monkeys' heads were approximately 60 cm apart, and these positions were maintained for roughly 2 min. A digital video camera was held by an experimenter standing 2.5 m from the monkeys. To estimate the percentage of time that subjects looked toward each other, we used point sampling with 5 s intervals. For the first 20 point samples of each session (100 s), we scored subjects as looking directly toward the other monkey or not.

Mirror Experiment

While seated, monkeys were brought into a familiar experimental room and a full-length mirror (30 cm × 120 cm) was brought into close proximity to their faces (~20 cm) for roughly 2 min. The mirror was angled toward monkeys at 30°, which permitted an experimenter to videotape the monkey and its reflection simultaneously. We used point sampling to classify each mirror exposure for the occurrence of unambiguous submissive [19, 20] or aggressive [20] displays. To estimate the percentage of time that subjects looked toward their mirror image, we used point sampling with 5 s intervals. For the first 16 point samples of each session, we scored subjects as looking directly toward the mirror or not.

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