

Visual Kin Recognition in Nonhuman Primates: (*Pan troglodytes* and *Macaca mulatta*): Inbreeding Avoidance or Male Distinctiveness?

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Faces provide important information about identity, age, and even kinship. A previous study in chimpanzees reported greater similarity between the faces of mothers and sons compared with mothers and daughters, or unrelated individuals. This was interpreted as an inbreeding avoidance mechanism where females, the dispersing gender, should avoid mating with any male that resembles their mother. Alternatively, male faces may be more distinctive than female faces, biasing attention toward males. To test these hypotheses, chimpanzees and rhesus monkeys matched conspecifics' faces of unfamiliar mothers and fathers with their sons and daughters. Results showed no evidence of male distinctiveness, rather a cross-gender effect was found: chimpanzees were better matching moms with sons and fathers with daughters. Rhesus monkeys, however, showed an overwhelming bias toward male-distinctiveness. They were faster to learn male faces, performed better on father–offspring and parent–son trials, and were best matching fathers with sons. This suggests that for the rhesus monkey, inbreeding avoidance involves something other than facial phenotypic matching but that among chimpanzees, the visual recognition of facial similarities may play an important role.

Keywords: kin recognition, face, phenotypic matching, male distinctiveness, inbreeding

Faces are rich social stimuli for human and nonhuman primates providing information about individual identity, gender, age, and emotional state (Bruce et al., 1993; Maurer, Le Grand, & Mondloch, 2002; Parr, Waller, & Heintz, 2008; Parr, Winslow, Hopkins, & de Waal, 2000; Tanaka & Farah, 1993). In addition to these

cues, studies suggest that faces provide important visual information about the relatedness among individuals, a type of phenotypic matching. Among humans, Christensen and Hill (1995) first reported that 1-year-old infants show more facial resemblance to their biological fathers compared with their biological mothers, interpreted as a mechanism for assuring paternal investment. However, several subsequent studies raised concerns about this finding and instead reported greater perceptual similarity between mothers and newborns. McLain, Setters, Moulton, and Pratt (2000), for example, asked mothers and unrelated individuals to judge whether the faces of newborns were more similar to the biological mother or father. Mothers ascribed resemblance to the biological father more than themselves, supporting the Christenfeld and Hill (1995) findings, but unrelated individuals tended to match the newborns to photographs of the mothers more than the fathers. This suggests that the physical resemblance between newborns and mothers may actually be more striking than between babies and their fathers. Other studies have also failed to replicate the findings of Christenfeld and Hill (Bredart & French, 1999).

Almstrom and Knight (2005) argued that in previous studies examining parent–offspring resemblance, inappropriate control stimuli were used. Rather than compare the recognition of mothers and fathers with their offspring directly, Almstrom and Knight (2005) incorporated a control condition where males and females were paired randomly with unrelated offspring. Using a paired-associative learning task, they found significantly better performance for parent–offspring versus parent-unrelated trials, as would be expected. Of interest, subjects were faster overall learning the father–offspring trials than mother–offspring trials, but a

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specific comparison between these failed to produce significant differences. Detecting parent–offspring similarities is more likely to be based on the unique facial configurations of each parent, rather than a single feature (e.g., hair color, nose shape, etc.), which in many cases could be similar in both parents, or even in unrelated individuals. Moreover, these configural similarities appeared to be stronger, or more distinctive, in male faces than female faces.

From an evolutionary perspective, the ability to recognize kin from visual (facial) cues alone would confer considerable advantages to individuals when forming alliances, avoiding inbreeding, and providing care for family members other than immediate offspring. However, despite the evolutionary significance of a visual kin recognition mechanism among primates, very few studies have examined this question in any detail in nonhuman primates. Moreover, most of these studies are confounded by failing to control for the familiarity of individuals, independent of their relatedness. In one well-cited study, Dasser (1987) presented two macaques with the task of matching photographic images of related and unrelated group members based on visual similarities. One subject was able to do this, but for the familiar individuals only, which did not support a kin recognition explanation based solely on visual similarity, independent of familiarity. Other studies have examined kin recognition by measuring the preference of monkeys to associate with immediate kin members for example, from the same matriline, versus unrelated group members, although in both cases the individuals were familiar. These studies failed to support any additive effect of relatedness and only supported familiarity as a mechanism for producing social preferences in this species (Fredrickson & Sackett, 1984; MacKenzie, McGrew, & Chamove, 1985; Welker, Schwibbe, & Schafer-Witt, 1987). In a captive research environment, however, genetically related individuals, for example, siblings, may be separated and reared apart from their natal group. Then, at a later time, social preferences among these genetically related individuals can be examined in the absence of any familiarity between them. When these conditions are in place, baboons showed no preference to interact with kin compared with nonkin (Erhart, Coelho, & Bramblett, 1997). These authors concluded that among nonhuman primates, learning about social relationships remains a more likely mechanism for kin recognition than an assessment of phenotypic similarity.

Parr and de Waal (1999) used a computerized, matching-to-sample (MTS) task to examine visual kin recognition in chimpanzees based solely on the facial similarity, independent of familiarity. Two female and three male subjects were presented with the task of matching the photographs of unfamiliar conspecifics combined into four types of trials, those in which the correct pair were different photographs of the same individual (e.g., individual recognition, or IR, trials), trials where the correct pair showed photographs of mothers and their offspring, either sons (MS trials) or daughters (MD trials), and trials showing three unrelated individuals (UC trials). No differences were found in subjects' ability to match IR and MS trials, or MD and UC trials, but subjects performed significantly better on MS trials compared with MD trials. Thus, subjects saw as much similarity in the faces of mothers and sons as two photographs of the same individual, and saw no more similarity in the faces of mothers and daughters than the faces of two unrelated individuals (Parr & de Waal, 1999).

These data suggest a type of phenotypic matching of related, but unfamiliar, individuals based solely on facial similarity and a stronger bias toward recognizing these features in male faces (sons). This bias might serve as a potential inbreeding avoidance mechanism where females, who are the dispersing gender in chimpanzees, avoid mating with extragroup males that resemble their mother.

The present study aimed to conduct a more inclusive test of visual kin recognition in nonhuman primates by presenting chimpanzees and rhesus monkeys with the task of matching unfamiliar mothers and fathers with their male and female offspring. If phenotypic matching of unfamiliar conspecific's faces is strictly associated with an inbreeding avoidance mechanism, chimpanzees are expected show better performance matching the faces of mothers and sons, as previously reported (Parr & de Waal, 1999), but rhesus monkeys should show greater recognition of mothers and daughters. This is because males, who are the dispersing gender in rhesus macaques, would benefit from avoiding mating with females who resembled their mothers. Poorer performance would be expected for fathers and offspring in both species as they each have promiscuous mating systems and paternity is unknown (Muller et al., 2007, but see Lehmann & Perrin, 2003).

The alternative, but not mutually exclusive, hypothesis is that successful matching of parents to offspring faces may be the result of their individual distinctiveness. Among humans, for example, male faces are more distinctive than female faces attributable, in part, to the prominent shape of the jaw and brow (Bruce et al., 1993; Fellous, 1997), and these cues are relatively impervious to degradation. The categorization of male faces from photographs, for example, persists even after the faces have been visually degraded from 28,000 to under 200 pixels, whereas the categorization of female faces deteriorates to chance levels when the faces are degraded only to 1,800 pixels (Cellerino, Borghetti, & Sartucci, 2004). Moreover, when superficial features such as hair lines and skin texture are removed, significantly more errors are made discriminating female compared with male faces (Bruce et al., 1993). If male facial characteristics are sexually selected among primates, then there should be greater similarity between the traits of fathers and offspring compared with mothers and offspring. This would increase the distinctiveness of male facial features and enhance the recognition of related males. Therefore, in contrast to the inbreeding avoidance hypothesis, the male-distinctiveness hypothesis would predict that both monkeys and apes should detect the greatest similarity between fathers and sons and the least similarity between mothers and daughters, where visual similarity between fathers and daughters and mothers and sons is expected to be more or less comparable and fall somewhere in between.

Method

Subjects

Six chimpanzees (four males and 2 females, 15–19 years old) participated in these studies; five were the same as those used in Parr & de Waal, 1999. They were all born at the Yerkes National Primate Research Center and raised by humans in peer groups until 4s years of age. This provided them with appropriate peer contact and social interaction early in their development. All subjects had

prior experience with a range of computerized tasks using MTS procedures, including face recognition tasks (Parr et al., 2000).

Seven rhesus monkeys (two males and 5 females, 6–7 years old) participated in these studies. They were born at the Yerkes National Primate Research Center's field station in large social groups until approximately 4 years of age when they were paired and moved to the main facility for participation in these studies. These rhesus monkeys also had considerable experience with computerized tasks using a MTS format before participating in these studies. This included matching unfamiliar faces and facial expressions (Parr, Heintz, & Pradhan, 2008; Parr & Heintz, 2009).

Stimuli and Testing Procedure

Stimuli consisted of black and white photographs of unfamiliar conspecific's faces. Chimpanzee face photographs were taken of individuals living at the Yerkes National Primate Research Center, Atlanta, Georgia; and in cooperation with the MD Anderson Cancer Center in Bastrop, Texas; the Detroit Zoo, Detroit, Michigan; the John Ball Zoo, Grand Rapids, Michigan; the Toledo Zoo, Toledo, Ohio; the Lincoln Park Zoo, Chicago; and from the archives of the Jane Goodall Institute showing chimpanzees living in Gombe National Park, Tanzania. Relatedness among these individuals was determined by the facility in which they were located using either known information about housing condition and colony records (Yerkes, John Ball Zoo, Detroit Zoo, Toledo Zoo, Lincoln Park Zoo), or direct DNA analyses (Gombe, Tanzania and Bastrop, TX). To provide more assurance that a nonmatching individual would not be related in any way to those in the matching (kin) pair, the nonmatching individual was always taken from a different colony. There was known relatedness among individuals in some of the zoo colonies but these were established prior to stimulus selection with the help of Steve Ross, Chair of the Chimpanzee Species Survival Plan (SSP). The authors are grateful to the staff and researchers at these facilities for allowing photographs of their animals to be used and for help in acquiring them.

The rhesus monkey face photographs were acquired primarily from colonies living at the Yerkes National Primate Research Center, Lawrenceville, Georgia, where detailed colony records and DNA paternity results were available. The paternity testing was done at the Southwest Foundation for biomedical research and only confirmed fathers were used (those sharing at least 10 loci with an infant and not sharing more than 2 loci with other potential sires). Only a small number of adult males are maintained in the Yerkes' breeding colony, so photographs of additional adult males were acquired from colonies living at the National Institutes of Health Animal Center in Poolesville, Maryland (courtesy of Dr. Annika Paukner), and from the colony living at the Caribbean Primate Research Center, Cayo Santiago, Puerto Rico (courtesy of Dr. Emily Bethell). None of these individuals are related to Yerkes monkeys, so they were used as nonmatching, unrelated individuals in all cases.

The photographs were cropped to show only the face. The background details were filled in using a grayscale tone in Adobe Photoshop 7.0. Only adult individuals were shown, approximately >8 years for chimpanzees and >4 years for rhesus monkeys. These faces were combined into four types of kin trials, mothers and daughters (MD), mothers and sons (MS), fathers and daughters (PD),¹ and fathers and sons (PS). Figures 1 and 2 show

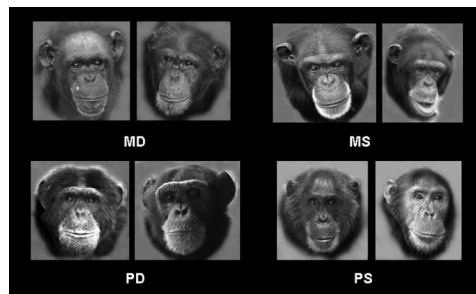


Figure 1. An illustration of the four kin trial types for chimpanzees.

examples of these trial types for chimpanzees and rhesus monkeys, respectively. The parent (mom or dad) was always the sample image (see details below), or the stimulus to be matched, and the offspring (son or daughter) was always the correct choice. The nonmatching image showed an individual unrelated to the kin pair but matched for the gender and approximate age of the offspring. Individuals were only used once, so if a mother or father had more than one offspring, only one was chosen for inclusion in the task and neither that parent nor that offspring was used again.

Chimpanzees were tested voluntarily in their home cage using a computerized, joystick-testing system and MTS format (Figure 3). Subjects were first required to orient to a single image on the monitor, hereafter referred to as the sample. Chimpanzees did this by contacting the sample with the joystick-controlled cursor. Monkeys were required to touch the sample image three times in rapid succession. Because the monkeys typically work at a much faster pace than the chimpanzees, this ensured that they looked at the sample stimulus. The location of the sample was randomly selected to appear against any of the four walls of the monitor, in a central location (top, left, bottom, or right side). After making the orienting response to the sample, two comparison images were presented in each corner of the touchscreen on the wall opposite to the sample, forming a triangular configuration. Subjects were then required to select the comparison image that matched the sample. For the experiments presented here, the sample image remained on the screen during the selection period (Figure 3b). If the response was correct, the subject would receive a food reward followed by an intertrial interval (ITI) of 2 s, while an incorrect response was followed by an ITI of 8 s and no food reinforcement. All procedures were approved by the Institutional Animal Care and Use Committee of Emory University.

Chimpanzees: Stimuli and Procedures

For the chimpanzees, there were five unique trials showing each of the four stimulus categories, mothers and daughters (MDkin), fathers and daughters (PDkin), mothers and sons (MSkin) and fathers and sons (PSkin) (Figure 1). These were presented in two phases that were counterbalanced across subjects. One phase showed parents with daughters (Daughters) and the second phase showed trials containing parents and sons (Sons). This was done to minimize the overall number of unique trials subjects viewed in a single testing session. In addition to these kin trials, there were two

¹ M stands for maternal and P stands for paternal.

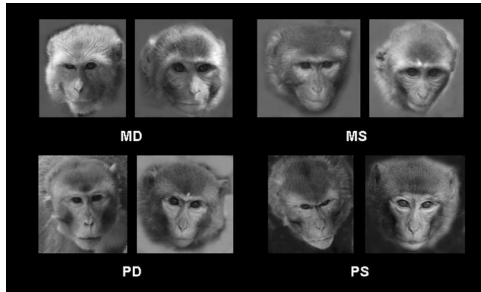


Figure 2. An illustration of the four kin trial types for rhesus monkeys.

sets of control trials, easy controls and hard controls. The easy controls paired two identical photographs of unfamiliar conspecifics as the matching pair (one trial each showing males and females), where the nonmatching photograph was another individual of the same gender category. The hard controls consisted of three different individuals (either all males or all females within a trial) where one was randomly assigned as the correct face and was reinforced if selected by the subject (similar to the procedures used in Parr & de Waal, 1999).

These 14 unique trials (5 mom–offspring, 5 dad–offspring, and the four control trials) were presented four times per testing session, totaling 56 trials per session. These were repeated on a daily basis until subjects performed above chance on either kin category (for the Daughter session, either MDkin or PDkin trials, or for the Son session, either MSkin or PSkin trials). Because there were five unique trials in each of the four kin categories and these were repeated 4 times per session, this required subjects to achieve 15/20 correct responses in a single session, or >75%. After this, they were moved on to the next set of kin trials, either Daughters or Sons, and testing continued using the same criteria. As a matter of replication, when these two sessions were completed, an identical task was presented that contained all novel examples of kin and control trials. In this replication task, the order of the kin sessions was counterbalanced so that if a subject had received Daughters first, they now started with Sons, but the same criteria procedures (>75%) applied.

Rhesus Monkeys: Stimuli and Procedures

Photographs showing the same four kin relationship categories (MDkin, MSkin, PDkin and PSkin), were compiled for rhesus monkeys (Figure 2). Our previous studies with these same subjects have confirmed a general difficulty that rhesus monkeys have matching faces based on individual identity (Parr, Heintz, & Pradhan, 2008), which is in contrast to the ease with which chimpanzees perform these face discriminations (Parr et al., 2000). Therefore, the format for testing the monkeys in this study differed from the chimpanzees in the following way: monkeys first learned to discriminate the parents themselves and then generalized this discrimination to the same photographs of parents but now matched to their offspring. To do this, individual recognition trials (IR) were presented in which the sample image showed the face of a male (father) or female (mother) monkey and the correct choice was another photograph of that same individual. The nonmatch, or foil, was a different, unrelated individual of the same gender and

approximate age class (Figure 3). This is the same format used to assess individual recognition in previous studies (Parr, Heintz, & Pradhan, 2008; Parr et al., 2000). For the present purposes, four separate IR tasks were presented each containing 10 unique trials showing the 10 adult females that would eventually be paired with daughters (MDlearn), the 10 adult females that would be paired with sons (MSlearn), 10 adult males that would be paired with daughters (PDlearn) and finally only 9 males could be identified where there were also pictures of sons, so PSlearn contained nine dads/males. Each learning category was presented separately and four repetitions of each trial were presented in a session (total 40 trials, or 36 for the PSlearn category) and subjects typically received two test sessions per day. As predicted, subjects had difficulty learning all 10 individuals, so training continued until performance was consistently (over 2 consecutive sessions) above 75% for at least five of the 10 parents in each category.

After reaching this criterion, unique kin tasks were prepared for each subject based on the five parents that they had succeeded in learning. The kin tasks contained 10 unique trials, the five previously learned parent trials (which now served as control trials), plus five kin trials in which same photographs of each previously learned parent was now paired with their respective offspring as the correct choice (MDkin, MSkin, PDkin, and PSkin). In these kin trials, the nonmatching foil was an unrelated individual the same gender and approximate age as the offspring (and always unique from any individual used during the learning trials). These 10 unique trials were repeated five times in a single session (total 50 trials) and subjects were given only two testing sessions before moving on to the next kin category (learning the next set of parents). All tasks were presented in the same order, MDlearn then MDkin, MSlearn then MSkin, PDlearn then PDkin, and PSlearn then PSkin.

Data Analysis

Chimpanzees. The data were analyzed by comparing the mean performance for each kin category on the session when subjects first exceeded chance performance on at least one category. For a 20-trial session, subjects were required to perform at least 15 correct out of 20 (75%), $z > 1.96$, two-tailed, $p < .05$. This was done using a repeated measures analysis of variance (ANOVA) where parent gender and offspring gender were the within-subject variables. Follow-up comparisons were performed where appropriate using paired t tests.

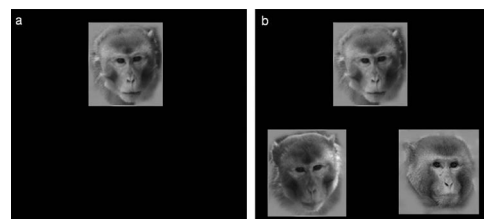


Figure 3. An illustration of the matching-to-sample (MTS) procedure. In (a) subjects orient to the sample image, and adult male. Once contacted, two comparison images appear (b) and subjects must select the comparison image that most resembles the sample. The correct choice is the face on the left, another photograph of the sample male (a), and the nonmatch is an unrelated male of same approximate age.

Rhesus monkeys. First, it was important to demonstrate that subjects performed comparably on the two sets of parent stimuli used for each offspring category, so paired *t* tests were used to compare the number of trials required before monkeys performed above chance on each set of maternal, MDlearn versus MSlearn, and paternal face sets, PDlearn versus PSlearn. Performance was required to be >65.5% on a 40 trial session to exceed chance, $p < .05$. Subjects saw each stimulus 4 times in a single session, so the minimum number of trials before chance could be exceeded was 4. Second, it was important to evaluate whether monkeys performed differently learning the faces of females (moms) versus males (dads) in general. Thus, paired *t* tests compared the number of trials needed before subjects reached criterion on the maternal learning trials (MDlearn + MSlearn = M-learn) compared with the paternal learning trials (PDlearn + PSlearn = P-learn). Finally, a repeated measures ANOVA compared monkeys' performance on the four kin trials where parent gender, offspring gender, and trial session were the within-subject factors. Follow-up comparisons were performed where appropriate. All statistics are reported as 2-tailed with a significance of $p < .05$.

Results

Chimpanzees

Initially, a full factorial model was used to determine whether performance differed between the easy (matching identical photographs) and hard (matching unrelated individuals) control trials. Within-subject factors included trial type (easy vs. hard), gender of faces (males vs. female faces), and replication task (Task 1 vs. replication task). This resulted in a single significant main effect for trial type, $F(1, 5) = 6.56, p = .05$. Subjects were significantly better matching pictures of the identical photographs in the easy controls ($M = 83.85\%$, $SEM = 5.38$) compared with pictures of unrelated individuals in the hard controls ($M = 68.75\%$, $SEM = 4.03$). Paired *t* tests were used to compare the number of trials required before subjects' performance exceeded chance on the Daughter sessions versus the Sons sessions. This resulted in no significant differences for either the first task, $t(5) = 0.97, p = .38$, or the replication, $t(5) = 1.35, p = .24$.

Next, a repeated measures ANOVA was performed for each task replication separately using parent gender (moms vs. dads) and offspring gender (sons vs. daughters) as the within-subject factors. This revealed a significant interaction between parent and offspring gender in Task 1, $F(1, 5) = 8.81, p < .04$, but not the replication task, $F(1, 5) = 0.25, p = .64$. Subjects were significantly better matching fathers and daughters (PDkin) compared with fathers and sons (PSkin), $t(5) = 4.03, p < .01$, and significantly better matching mothers and sons (MSkin) compared with fathers and sons (PSkin), $t(5) = 2.78, p < .04$ (Figure 4). Table 1 lists subjects' individual performance on each kin category summed across both tasks.

Rhesus Monkeys

No significant differences were found in the number of trials required before monkeys exceeded chance performance (>65.5%) on a single session of individual recognition trials involving moms; MDlearn ($M = 26.29, SEM = 4.85$) versus MSlearn ($M =$

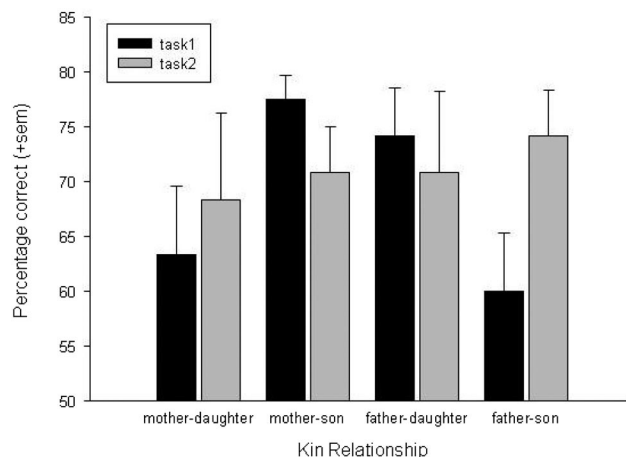


Figure 4. Mean performance by chimpanzees matching each of the four kin categories in the first task and replication.

18.29, $SEM = 3.13$) compared with dads; PDlearn ($M = 5.71, SEM = 1.19$) versus PSlearn ($M = 7.43, SEM = 0.57$) trials. Therefore, the general quality of the parent images was consistent across the two offspring categories. However, monkeys learned the individual recognition trials involving fathers (P-learn, $M = 6.57, SEM = 0.72$) significantly faster than those trials involving mothers (M-learn, $M = 22.29, SEM = 1.60$), $t(6) = 7.00, p < .001$. Thus, overall male faces were much easier to discriminate than female faces.

Table 2 lists subjects' individual performance on each kin category. Differences in kin recognition were assessed using a repeated measures ANOVA where parent gender (moms vs. dads), offspring gender (daughters vs. sons), and testing session (Session 1 vs. Session 2) were the within-subject factors. This revealed a significant main effect of parent gender, $F(1, 6) = 6.01, p < .05$, where subjects were significantly better matching paternal kin ($M = 73.25\%$, $SEM = 3.85$) versus maternal kin ($M = 63.10\%$, $SEM = 2.06$), and a significant main effect of offspring gender, $F(1, 6) = 12.98, p < .02$, where subjects were significantly better matching parents to sons ($M = 73.64\%$, $SEM = 1.85$) versus parents to daughters ($M = 62.70\%$, $SEM = 3.41$). No other main effect or interaction was significant. Moreover, linear contrasts revealed no significant effect of trial order, suggesting no overall learning with task repetition, $F(1, 6) = 1.63, p = .25$. Figure 5 shows the mean percent correct (+SEM) matching each category of kin trial.

Discussion

The goal of this study was to compare and contrast visual kin recognition mechanisms in chimpanzees and rhesus monkeys. In a previous study, Parr and de Waal (1999) reported greater visual similarity between the faces of mothers and sons compared with mothers and daughters or unrelated individuals (Parr & de Waal, 1999). This was interpreted as an inbreeding avoidance mechanism where females, who are the dispersing gender in chimpanzees, avoid mating with males that resemble their mothers. If this was the primary explanation underlying phenotypic kin matching, then rhesus monkeys would be expected to show greater recognition of

Table 1
Individual Chimpanzee's Performance on Each Kin Category

Subject		Kin trial category			
Name	Gender	MD	MS	PD	PS
Jarred	M	55.0	72.5	77.5	70.0
Lamar	M	62.5	80.0	85.0	62.5
Scott	M	80.0	77.5	65.0	65.0
Patrick	M	72.5	70.0	82.5	77.5
Katrina	F	70.0	67.5	60.0	77.5
Faye	F	55.0	77.5	65.0	50.0
Male chimpanzees		67.5	75.0	77.5	68.8
Female chimpanzees		62.5	72.5	62.5	63.8

Note. MD = mother-daughter; MS = mother-son; PD = father-daughter; PS = father-son; M = male; F = female.

mothers and sons, as males are the dispersing gender in rhesus monkeys and males would be aided by avoiding mating with females who resemble their mothers. An alternative explanation, however, remained that, as in humans, male faces may simply be more distinctive and thus more interesting, or attractive, than female faces which could have biased the original chimpanzee results toward better discrimination of sons' faces. The present study included the faces of fathers and offspring, in addition to mothers and offspring, providing an opportunity to test this alternative, male-distinctiveness hypothesis.

In this study, the previous mother-son bias for chimpanzee faces was partially replicated. Chimpanzees were significantly better matching the faces of mothers and sons compared with mothers and daughters, in Task 1 only, supporting the inbreeding avoidance explanation. However, also observed in the first stimulus set was an unexpected cross-gender effect in that subjects showed better performance matching the faces of fathers and daughters compared with fathers and sons. A breakdown of these data by the gender of the chimpanzee subjects showed that this cross-gender effect appears to be driven by the male subjects, as they individually performed as well or outperformed the two female subjects. Although this result is interesting, a visually based inbreeding avoidance mechanism specific to males would predict better recognition of mothers and daughters, where philopatric males avoid mating

Table 2
Individual Rhesus Monkey's Performance on Each Kin Category

Subject		Kin trial category			
Name	Gender	MD	MS	PD	PS
Samosa	M	68.3	74.0	83.5	78.0
Rocket	M	56.0	72.0	70.0	86.0
Onion	F	46.0	72.0	68.0	80.0
Olive	F	58.0	74.0	46.0	68.0
Chewy	F	70.0	50.0	44.0	78.0
Lemon	F	76.0	57.0	72.0	94.0
Caramel	F	42.0	68.0	78.0	80.0
Male rhesus monkeys		62.2	73.0	76.8	82.0
Female rhesus monkeys		58.4	64.2	61.6	80.0

Note. MD = mother-daughter; MS = mother-son; PD = father-daughter; PS = father-son; M = male; F = female.

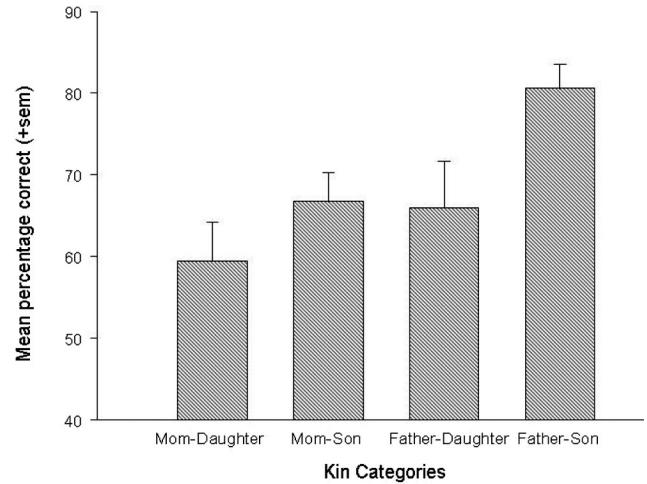


Figure 5. Mean performance by rhesus monkeys matching each of the four kin categories.

with females that remain in the natal group. It is unclear what this cross-gender effect means or if it can be replicated in future experiments. In no instance, however, do the chimpanzee data provide support for the alternative hypothesis of male-distinctiveness in this species, despite prominent sexual dimorphism in chimpanzee facial shape (Schmittbuhl, Le Minor, Allenbach, & Schaaf, 1999).

Overall, there did not appear to be any order effects that could explain why the cross-gender advantages found in Task 1 were not replicated in the second experiment. There was, for example, no overall improvement in matching kin faces from Task 1 to the replication task: Task 1 was 69% compared with 71% in the replication, so no effect of learning was observed. Instead, the performance was more uniform across kin categories in the replication task than in Task 1. So, if order effects were present, and subjects were simply better at kin discrimination by the time the replication task was presented, these effects were greater for some kin categories than others which seems only weakly plausible. Perhaps unintentional biases in the selection of the images themselves had occurred prior to testing. However, on reexamination, all individuals' whose faces were shown to subjects were unfamiliar. Each photograph was preprocessed to provide the most homogeneous stimulus set for this type of study. Images were all adjusted for brightness and contrast, cropped to reveal only the face and standardized in terms of size. Each image was selected on the basis of kin category only, not on the task in which they would be used. The individuals presented in the tasks were well distributed across their colony of origin, so distinctiveness specific to a particular colony could not account for the differences in performance. In the two tasks, for example, there were a total of 15 versus 13 individuals selected from the chimpanzee colony in Bastrop, Texas, 7 versus 10 individuals selected from Gombe National Park, Tanzania, 7 versus 4 individuals selected from the Chester Zoo, United Kingdom, 7 versus 8 selected from a combined category including the Detroit Zoo, Lincoln Park Zoo, and John Ball Zoo, and finally 4 versus 5 individuals selected from the Yerkes' colony. Because these tasks rely on untrained perceptual preferences that detect similarity in some images over others, that

the presentation of images back to back shifted their strategies and minimized these perceptual preferences. Only subsequent experiments using novel images can help to explain these results. Moreover, any future study should attempt to measure the physiognomic similarities between the faces of related compared with unrelated individuals and then correlate performance based on actual physical resemblances. This is extremely difficult to do because the faces would need to be as full frontal as possible, however, even a unilateral series of measurements may shed some light on these issues.

In contrast to the chimpanzees, the results from the rhesus monkeys failed to provide any support of an inbreeding avoidance hypothesis. Of the four kin categories, they performed the worst on the mother–daughter trials, the one predicted to be best if an inbreeding avoidance mechanism were a likely explanation. Instead, the data strongly supported the male-distinctiveness hypothesis. Not only did the monkeys learn to discriminate the male faces (all fathers) faster than the female faces (all mothers), they showed significantly better recognition of fathers and offspring compared with mothers and offspring, and for all son trials compared with daughter trials, regardless of parent gender. The best recognition was for photographs of fathers and sons. The monkeys were tested on each kin category in the same order (mothers–daughters, mothers–sons, fathers–daughters, and finally fathers–sons), leaving open the possibility for an order effect, for example, the best performance was for the category tested last, fathers–sons. There are, however, several lines of evidence suggesting that male distinctiveness, rather than order effects, provide the most reasonable explanation for these data. First, there was no linear improvement in performance from the first to the last kin category, suggesting no overall improvement across the four kin categories with repeated testing. There was no significant interaction between parent and offspring gender, so subjects did not perform better on PSkin trials than PDkin trials even though PSkin trials were presented last, nor was performance on MSkin trials better than PSkin trials, even though MSkin trials were presented second and the PSkin trials were presented last. Finally, it took subjects slightly longer to learn the PDlearn male faces compared with the PSlearn male faces, despite the fact that the PSlearn male faces were presented last. Thus, on further examination, the face gender rather than trial order provide the best explanation for these results. As discussed above, devising a means for measuring the distinctiveness of nonhuman primate faces that vary in their head orientation and viewpoint would help shed some light on the distinctiveness of male versus female faces.

Previous studies, both empirical and theoretical, have shown that male dispersal is a primary means for reducing female inbreeding in animal species (Perrin & Mazalov, 2000). Among mammals, for example, males are typically the dispersing gender (Pusey & Packer, 1987). For rhesus monkeys, male migration may effectively reduce the costs of female inbreeding such that any additional mechanism would have little or no added benefits. It has been shown, however, that in the presence of specific kin recognition mechanisms among females, the pattern of male dispersal may change (Lehmann & Perrin, 2003). This pattern of dispersal may lead males to become more philopatric, a situation that is common among chimpanzees, where males remain in their natal group and females typically disperse. In this case, females would be aided by a visual kin recognition mechanism where they avoid

mating with extragroup males that resemble their mothers (Parr & de Waal, 1999). However, recent genetic studies across most of the major, long-term chimpanzee field sites in Africa show that female dispersal among chimpanzees is not always clear (Gombe National Park, Tanzania: Pusey, Williams, & Goodall, 1997; Tai Forest, Ivory Coast: Boesch & Boesch-Achermann, 2000; Kibale Forest, Uganda: Kahlenberg, Emery, Thompson, & Wrangham, 2008; Mahale National Park, Tanzania: Nishida et al., 2003) and, in documented cases, females may remain in their group and gain protection from resident males with whom they have known relationships (Gagneux, Boesch, & Woodruff, 1999). Studies of genetic relatedness among several groups of wild African chimpanzees have shown that over 82% of offspring had a father living within the same community, and one confirmed birth from an extragroup male (Vigilant, Hofreiter, Siedel, & Coesch, 2001). This creates additional problems among females to avoid mating with related males within their same community. Yet in light of the risk of inbreeding in these situations, there has been only one documented birth between related individuals, a mother and son (Constable, Ashley, Goodall, & Pusey, 2001; Wroblewski et al., in press). These genetic data confirm that, despite flexible migration patterns, female chimpanzees are able to successfully avoid inbreeding with closely related males in their community (Inoue, Inoue-Murayama, Vigilant, Takenaka, & Nishida, 2008). The present data suggest that this may be achieved through a combination of cues, such as visually based phenotypic matching, but it is also likely that familiarity and patterns of association may play a role. In contrast, rhesus monkeys show a strong discrimination advantage for male faces, whether this be learning to match male faces (in the individual recognition training trials) or matching the faces of males kin (fathers and offspring or parent and sons). This provides strong support for the male-distinctiveness hypothesis in this species and does not support a primate-wide mechanism for inbreeding avoidance based on phenotypic matching of faces.

References

- Almstrom, C., & Knight, M. (2005). Using a paired-associate learning task to assess parent-child phenotypic similarity. *Psychology Reports, 97*, 129–137.
- Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai Forest*. Oxford, United Kingdom: Oxford University Press.
- Bredart, S., & French, R. M. (1999). Do babies resemble their fathers more than their mothers? A failure to replicate Christenfeld and Hill 1995. *Evolution and Human Behavior, 28*, 129–135.
- Bruce, V., Burton, A. M., Hanna, E., Healey, P., Mason, O., Coombes, A., Fright, R., & Linney, A. (1993). Sex discrimination: How do we tell the difference between male and female faces? *Perception, 22*, 131–152.
- Cellerino, A., Borghetti, D., & Sartucci, F. (2004). Sex differences in face gender recognition in humans. *Brain Research Bulletin, 63*, 443–449.
- Christenfeld, N. J. S., & Hill, E. A. (1995). Whose baby are you? *Nature, 378*, 669.
- Constable, J. L., Ashley, M. V., Goodall, J., & Pusey, A. E. (2001). Noninvasive paternity assignment in Gombe chimpanzees. *Molecular Ecology, 10*, 1279–1300.
- Dasser, V. (1987). Slides of group members as representations of the real animals (*Macaca fascicularis*). *Ethology, 76*, 65–75.
- Erhart, E. M., Coelho, A. M., & Bramblett, C. A. (1997). Kin recognition by paternal half-siblings in captive *Papio cynocephalus*. *American Journal of Primatology, 43*, 147–157.
- Fellous, J. (1997). Gender discrimination and prediction on the basis of facial metric information. *Vision Research, 37*, 1961–1997.

- Fredrickson, W. T., & Sackett, G. P. (1984). Kin preferences in primates (*Macaca nemestrina*): Relatedness or familiarity? *Journal of Comparative Psychology*, *98*, 29–34.
- Gagneux, P., Boesch, C., & Woodruff, D. S. (1999). Female reproductive strategies, paternity and community structure in wild West African chimpanzees. *Animal Behaviour*, *59*, 19–32.
- Inoue, E., Inoue-Murayama, M., Vigilant, L., Takenaka, O., & Nishida, T. (2008). Relatedness in wild chimpanzees: Influence of paternity, male philopatry, and demographic factors. *American Journal of Physical Anthropology*, *137*, 256–262.
- Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2008). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology*, *29*, 931–947.
- Lehmann, L., & Perrin, N. (2003). Inbreeding avoidance through kin recognition: Choosy females boost male dispersal. *American Naturalist*, *162*, 638–652.
- MacKenzie, M. M., McGrew, W. C., & Chamove, A. S. (1984). Social preferences in stump-tailed macaques (*Macaca arctoides*): Effects of companionship, kinship, and rearing. *Developmental Psychobiology*, *18*, 115–123.
- Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Science*, *6*, 255–260.
- McLain, D. K., Setters, D., Moulton, M. P., & Pratt, A. E. (2000). Ascription of resemblance of newborns by parents and nonrelatives. *Evolution and Human Behavior*, *21*, 11–23.
- Muller, M. N., Kahlenberg, S. M., Emery-Thompson, M., & Wrangham, R. W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society of London: B*, *274*, 1009–1014.
- Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., . . . Zamma, K. (2003). Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology*, *59*, 99–121.
- Parr, L. A., & de Waal, F. B. M. (1999). Visual kin recognition in chimpanzees. *Nature*, *399*, 647–648.
- Parr, L. A., Heintz, M., & Pradhan, G. (2008). Rhesus monkeys (*Macaca mulatta*) lack face expertise. *Journal of Comparative Psychology*, *122*, 390–402.
- Parr, L. A., Waller, B. M., & Heintz, M. (2008). Facial expression categorization by chimpanzees using standardized stimuli. *Emotion*, *8*, 216–231.
- Parr, L. A., Winslow, J. T., Hopkins, W. D., & de Waal, F. B. M. (2000). Recognizing facial cues: Individual recognition in chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, *117*, 47–60.
- Parr, L. A., & Heintz, M. (2009). Facial expression recognition in rhesus monkeys. *Animal Behaviour*, *77*, 1507–1513.
- Perrin, N., & Mazalov, V. V. (2000). Local competition, inbreeding, and the evolution of sex-biased dispersal. *American Naturalist*, *155*, 116–127.
- Pusey, A., & Packer, C. (1987). Dispersal and philopatry. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Strusaker (Eds.), *Primate societies* (pp. 250–266). Chicago: The Chicago University Press.
- Pusey, A., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, *277*, 828–831.
- Schmittbuhl, M. S., Le Minor, J. M., Allenbach, B., & Schaaf, A. (1999). Shape of the orbital opening: Individual characterization and analysis of variability in modern humans, *Gorilla gorilla* and *Pan troglodytes*. *Annals of Anatomy*, *181*, 299–307.
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology*, *46A*, 225–245.
- Vigilant, L., Hofreiter, M., Siedel, H., & Coesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academies of Science USA*, *98*, 12890–12895.
- Welker, C., Schwibbe, M. H., & Schafer-Witt, C. (1987). Failure of kin recognition in *Macaca fascicularis*. *Folia Primatologica*, *49*, 216–221.
- Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (in press). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*.

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