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Visual Discrimination of Kin in Mandrills

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Abstract

Phenotype matching, a learning mechanism that evolved based on phenotypic cues shared among relatives, may provide animals with the ability to recognize unfamiliar kin. The generalization of this mechanism across animal species is debated, however, because appropriate tests are difficult to design due to possible confounding effects of familiarity. Hence, only a few studies have examined evidence for the existence of such a mechanism in natural populations. Here, we tested the phenotype matching hypothesis based on visual cues in a semi-free-ranging population of mandrills (*Mandrillus sphinx*) that contains individuals related to different degrees and where familiarity is controlled for. Using an experimental design based on the presentation of photographs, we show that mandrills discriminate unfamiliar relatives using facial cues alone. Our results build on earlier studies, showing that primates use phenotype matching to recognize and subsequently discriminate unfamiliar kin. We suggest that facial features along with other visual and non-visual cues provide a proximate mechanism for kin selection to operate.

Introduction

In many animal species, facial features provide information on individual characteristics such as identity, sex or age (e.g., Bruce 1983; Bruce & Young 1986; Parr et al. 2000; Sheehan & Tibbetts 2011). In humans, several studies have suggested that the evaluation of facial characteristics plays a role in multiple contexts, including assessment of same-sex attractiveness (DeBruine 2004) or parent–offspring relationships (Platek et al. 2003; Alvergne et al. 2009, 2010). Humans are able to evaluate kinship based on facial resemblance (Dal Martello & Maloney 2006; DeBruine et al. 2009) and can even differentiate among individuals with different degrees of genetic relatedness (Kaminski et al. 2009). This human ability is shared with diverse non-human primate species: mother–offspring pairs in chimpanzees *Pan troglodytes* (Vokey et al. 2004; Alvergne et al. 2009), mother–offspring pairs in gorillas *Gorilla gorilla gorilla* (Alvergne et al. 2009), mother–daughter pairs in mandrills *Mandrillus sphinx* (Alvergne et al. 2009) and parent–offspring pairs in rhesus macaques *Macaca mulatta*: (Kazem & Widdig 2013).

Some non-human primates can also detect kin relationships by comparing pictures of conspecifics. After an extensive training period, captive chimpanzees and rhesus macaques matched faces of unfamiliar mothers and fathers with their corresponding sons and daughters (Parr et al. 2010). Moreover, free-ranging rhesus macaques spontaneously discriminated images of the faces of their own paternal half-siblings from those of unrelated individuals, particularly when the pictured animals were of the same sex as the subjects performing the task (Pfefferle et al. 2014). Because the macaques that provided the stimuli did not live in the same social group as the subjects, the latter study suggests that relatives do not have to be directly familiar with each other for kin recognition to operate. Kin recognition (here and below, recognition is considered in its broad sense, following: (Penn & Frommen 2010) without direct familiarity (emerging from prior, social and/or familial association) may involve phenotype matching mechanisms where individuals recognize, also through learning processes, unfamiliar or not directly familiar individuals as kin either by comparing their own phenotypes (self-referent phenotype matching or 'armpit effect'; Hauber & Sherman 2001) or those of known (directly familiar) kin with phenotypes of these evaluated kin (see definition in: Penn & Frommen 2010). Cues to recognize not directly familiar kin may be diverse, including body odors, acoustic features or personality traits.

Phenotype matching has been only rarely proposed as a possible mechanism responsible for kin recognition in primates (see for review: Widdig 2007), probably because kin relationships have been largely studied in matrilineal societies of Old World cercopithecines (Berman & Chapais 2004). In these societies, maternal kin generally grow up together and direct familiarity, where phenotypes are directly learned thanks to prior association, appears to be a 'sufficient' mechanism to recognize kin. However, some primate groups also contain numerous relatives that are not directly familiar with each other. For example, social groups of several species of Old World primates may contain numerous paternal half-sibs (sired by a same male), where the number depends on the reproductive skew among males (see for review: Widdig 2013). Because paternal half-sibs are generally born into different matrilines, they are not directly familiar with each other. For those individuals, mechanisms such as phenotype matching would allow minimizing the risks of incorrect kin detection, favoring the emergence of, for example, nepotism, inbreeding avoidance behavior and establishment of differentiated father–offspring relationships.

In primates, evidence for kin recognition among not directly familiar kin is mixed (see for review: Widdig 2007). For example, in wild chimpanzees, members of the majority of highly affiliative and cooperative pairs are unrelated, and paternal brothers do not selectively affiliate and cooperate with each other (Langergraber et al. 2007). Similarly, paternal half-sisters in white-faced capuchins (*Cebus capucinus*) do not associate more often than distantly related pairs of females (Perry et al. 2008). In contrast, in free-ranging rhesus macaques and wild yellow baboons (*Papio cynocephalus*), adult females affiliate more with their paternal half-sisters than unrelated females (Silk et al. 2006; Smith et al. 2003; Widdig et al. 2001, 2002; and see for review in other primates: Widdig 2007). These contrasting findings, rather than questioning the validity or pervasive nature of social biases among unfamiliar (or not directly familiar) kin primates, such as paternal kin (as per: Chapais 2001; Rendall 2004), may reflect responses to different selective forces, including the risks posed by inbreeding, male reproductive skew, kin availability and patterns of sex-biased dispersal.

While testing phenotype matching in natural populations of primates has been historically hampered by the necessity to tease apart the confounding effects of direct familiarity and kinship, experiments allow behavioral tests with related individuals with no or little prior social experience. In addition to discrimination of paternal half-sibs based on facial cues in rhesus macaques (Pfefferle et al. 2014), female rhesus macaques also discriminate unfamiliar paternal half-sisters during playback experiments based on vocal cues (Pfefferle et al. 2013). As a result of such experiments, there is now convincing evidence that phenotype matching may allow primates to perform kin-oriented decisions.

Mandrills are a forest-dwelling primates inhabiting dense equatorial African forests (Abernethy et al. 2002). These Old World monkeys live in large bisexual groups characterized by female philopatry and male natal and secondary dispersal (Abernethy et al. 2002; Brockmeyer et al. 2015). Reproduction is highly seasonal in the wild, with about two-thirds of females giving birth between December and February (MJEC, unpubl. data). Sexual dimorphism is extreme in mandrills, with males being more than three times heavier than females (Setchell et al. 2001) and showing bright facial and sexual coloration (Setchell & Dixson 2001). Competition between males is intense, resulting in alpha males' monopolization of reproduction in semi-free-ranging groups (Charpentier et al. 2005). As a consequence of this high reproductive skew, most new-born infants (70% on average: Charpentier et al. 2005) are related through the paternal line. However, because most of them are born into different matrilines, they are not directly familiar with each other. Yet, juvenile mandrills affiliate more with adult paternal relatives (half-sibs and father) than with non-kin (Charpentier et al. 2007), suggesting that mechanisms of kin recognition may exist. In a previous study, we demonstrated in a natural and a semi-free-ranging population that genetic relatedness is encoded in mandrills' contact calls and that captive mandrills discriminate unfamiliar kin, with no prior association, based on these calls alone (Levréro et al. 2015). Using similar experiments, we expand these previous studies by testing the phenotype matching hypothesis based on visual cues in a semi-free-ranging population of mandrills containing individuals with various degrees of relatedness and familiarity.

Materials and Methods

Study Subjects

We studied two mandrill populations living in Southern Gabon. One population was composed of about 200 individuals housed at a medical research centre (CIRMF; 'captive population' thereafter). This population consisted of three large social groups inhabiting natural habitat enclosures of 0.5–3.5 ha as well as of two small groups composed of 3–5 individuals housed in smaller enclosures (for details, see Levréro et al. 2015). These 200 animals originated from 14 wild unrelated male and female founders that arrived at CIRMF in the 1980s (Charpentier et al. 2005; Setchell et al. 2005a). We studied another natural population of about 130 individuals housed in a private park (Parc de la Lékédi, Bakoumba; 'natural population' thereafter), which originated from the CIRMF population following two release events in 2002 and 2006 (for details, see Peignot et al. 2008; Brockmeyer et al. 2015). Starting in 2002, wild males joined the group and began to reproduce, and by 2015 more than 85% of the individuals from this population were wild-born animals. Individuals from these two populations are habituated to human presence and are almost all individually recognized by trained observers. Regular censuses allowed determining the exact age of most study individuals. Animals from the natural population that were born before regular monitoring, which started in early 2012 (Brockmeyer et al. 2015), were assigned an estimated age based on general condition (a combination of size, stature and signs of senescence) and for some of them, patterns of tooth eruption and wear (Galbany et al. 2014).

For the purpose of the present study (and see below), eight individuals from the captive population were photographed ('donors') and their pictures were used during behavioral tests performed on 20 other animals from this population ('actors'). Nine animals from the natural population served as additional stimulus donors.

Determination of Relatedness and Familiarity Between Animals

Individuals from the two study populations were regularly captured using blowpipe intramuscular injections of anesthetics (Charpentier et al. 2005; Galbany et al. 2014), and blood samples were collected on every occasion. DNA extractions from the buffy coat (white cells) were performed using QIAamp DNA Blood Mini Kits (Hilden, Germany), and microsatellite genotyping was carried out using 12 (captive population; Charpentier et al. 2005) to 36 (natural population; Benoit et al. 2014) primer pairs. Paternity analyses were performed using Cervus 3.0 software using previously described procedures (Charpentier et al. 2005).

For the captive population, we reconstructed the full pedigree of all studied individuals, going back as far as the generation of the unrelated founder animals. We also reconstructed the full pedigree for all but one donor from the natural population. This particular donor was presumably fathered by a wild, unsampled male and was therefore possibly related to the actors only through the maternal line that was genetically determined. Individuals from both populations were related to each other to different degrees. However, because of the limited number of founders in these two populations, animals were of mixed genetic origin, i.e., they were related both through the maternal and the paternal lines. Consequently, we were able to analyze the impact of actor–donor genetic relatedness, which varied from r = 0 to 0.34 across all tests, on actor responses but not of kin categories because of these mixed ancestries.

We reconstructed the degree of familiarity between actors and donors using documented histories of cohabitation. Two individuals were considered as familiar when they experienced any form of social contact during any stage of their life. Familiar individuals spent between 6 months and 15 years together. In the following analyses, we considered the number of years living in the same social group rounded to the higher nearest integer as a conservative estimate of familiarity (see, for details, Levréro et al. 2015). Because of colony management, some related animals were raised apart and did therefore not experience any social contacts with each other (Levréro et al. 2015), allowing an unambiguous test of the phenotype matching hypothesis.

Behavioral Experiments

Image collection

We took color pictures (.jpeg) of donor faces in frontal position, with a neutral expression (mouth closed, eyebrows relaxed; Figure S1) using a digital camera (Nikon D7000). Donors were located 1–3 m away from the camera, and pictures were collected in the natural living environment of donors. Pictures were collected from 11 adult females (aged 3.6–19.1 yr; four from the captive population and seven from the natural one) and six non-mature males (aged 3.6–9.4 yr; four from the captive population and two from the natural one). We did not use pictures from adult male donors because prominent secondary sexual characteristics combined with possible confounding parameters linked to sexual selection may affect any relationship between behavioral biases and relatedness.

The 17 selected photographs were not post-processed. In particular, we chose to keep the natural background surrounding the head (in a central position) of the donors (Figure S1). Although the background varied between images, we are confident that this factor did not bias our results in any non-random direction. Indeed, the poor peripheral acuity of primate vision combined to center and face attentional biases during scene scanning (Birmingham et al. 2009) is likely to give little weight to non-facial features during evaluation of images by actors (but see Vokey et al. 2004). More importantly, 15/17 donors (88.2%) served both as the most related and as the least related donor across all the behavioral tests involving these donors. All pictures were printed in 21 × 29.7 cm format, roughly equating the size of a mandrill head, and were taped behind a protective sheet of plexiglass.

Behavioral tests

In June 2014 and May 2015, we performed a total of 39 tests on 20 adult actors from the captive population (11 males and nine females; 1–5 tests/actor; mean number of tests/actor: 1.95). All actors always performed their behavioral tests with different donor pictures. For each behavioral test, we offered pictures of either two adult females (n = 23 tests) or of two males (n = 16 tests) of varying degrees of relatedness and familiarity with the actors. The average difference of familiarity (with the actors) between the two donors was 2.1 years, and the average difference of genetic relatedness (with the actors) between the two donors was 0.13. Donor pictures were randomly positioned to the right or left of the test apparatus according to both familiarity and relatedness.

Tests were performed both on actors living in small social units and on individuals living in the semi-free-ranging enclosures. All tests occurred in the usual living quarters of the animals, all habituated to the test design, with tests taking place prior to feeding. When housed in small social units (n = 3 actors), we temporarily isolated the actor from its social companions for testing, using sliding doors and adjacent corrals. When housed in large enclosures (n = 17 actors), we also temporarily isolated actors in their cleaned feeding area composed of two parts (C1 and C2) connected through sliding doors. Prior to each test, actors entered into C1. Either in a corral or in C2, we attached two aligned stimulus photographs along the fence using wire. Pictures were located 2 m apart from each other and at about 20 cm or 50 cm above the ground for female and male actors, respectively. Each test started when one actor entered into the corral or into C2 and lasted 15 min.

Three trained observers, blind to the hypotheses being tested, were located in front of the actor and recorded the behavioral responses toward the two images using personal digit assistants which recorded time stamps and were especially designed for the present study. Actor responses were recorded by one observer at a time and included the time spent in proximity to each stimulus within a semicircle of 0.5 m in diameter around the picture (‘approach time’) as well as the total number of behaviors indicating interest (‘bouts of interest’), including gazing at the picture, touching it, smelling it or licking it. We analyzed all these behaviors in bouts, with two bouts of behavior being separated at least by a 3-sec time lag. When an actor performed more than one test (n = 13 actors), we allowed a 10-min period without any solicitations before setting up a new apparatus for a new test. In a few cases, actors (n = 4) were tested on several consecutive days.

Statistical analyses

We studied approach time as well as bouts of interest (both ln-transformed to fit normal distributions) as a function of different predictors, using general linear mixed models with a Gaussian error structure.

In the analyses, we first accounted for the genetic relatedness and familiarity of the actor–donor pairs. Here, and to avoid any biases linked to the possible bimodularity of these two predictors, some of the behavioral tests performed included two donors that were either both unrelated (n = 2 tests) or both unfamiliar (n = 22) to the actor. Second, we took into account actor and donor characteristics, including sex (M or F) and age (continuous variable in years). Finally, we considered in our analyses the number of times actors performed a test (continuous variable from 1 to 5) to control for possible habituation effects. In preliminary examinations of the data, the identity of the three observers was considered as a fixed categorical effect to quantify possible human biases. Furthermore, we explored possible effects of the position of the picture (right vs. left) to test for any lateralization preferences. These two variables were never found significant and were therefore not included in the final models.

In the initial LMM, we considered all first-order interactions involving genetic relatedness, our key predictor as well as the interaction between the two sexes of the pairs as well as their two ages. We kept final full models, excluding only non-significant interaction terms. In a second set of LMMs, we kept only those behavioral tests where both actor–donor pairs were unfamiliar with each other (n = 22 tests) and tested for the same possible effects. In all these analyses, we considered as a random effect the identity of the behavioral test performed. Identities of both actors and donors were not considered as additional random effects because of limited sample sizes. Including, however, the identity of either the actor or the donor as a random effect, rather than the identity of the behavioral test performed, did not change the results found (data not shown).

Ethics

This study complies with protocols approved by the CENAREST institution (authorization numbers: AR0001/14 and AR0018/15). The research adhered to the legal requirements of Gabon for the ethical treatment of non-human primates and was further approved by the local ethic committee (#0020/2013/SG/CNE).

Results

We found evidence that mandrill actors biased their behavior according to their genetic relatedness with pictured donors, but in combination with actor and donor characteristics (Table 1; see also Figure S2). When considering all tests, both the age of actors and donors influenced the relationships between the number of bouts of interest and relatedness: Older actors displayed a greater interest toward less related donors (Fig. 1a), and older unrelated donors elicited more interest than younger ones (Fig. 1b). While familiarity never influenced actor behavioral responses (Table 1), we found an additional effect of relatedness on approach time, but only among unfamiliar pairs: Both female and male actors spent more time in proximity to the pictures of more related males (Fig. 2a), but not females (Fig. 2b).

Finally, we found several effects of actor and donor features (Table 1): Male actors spent more time in proximity and investigated more pictures of female donors and the reverse pattern (female actors toward male donors) was also observed. Moreover, both older actors and donors displayed and elicited (respectively) more interest overall. Counterintuitively, we found that the number of tests performed by actors was positively correlated with the overall time spent in proximity to pictured donors (Table 1).

Discussion

In this study, we show that mandrills discriminate relatives based on visual cues obtained from conspecific's faces while controlling for prior social association (number of years spent in the same social group) that actors and donors experienced. Albeit our sample size is limited, due to the difficulty in designing such experiments in near-natural environments, we suggest that kin recognition (*sensu*: Penn & Frommen 2010) may occur in mandrills through mechanisms of phenotype matching because some of the behavioral tests included relatives that never met in their life. Recognition due to direct familiarity can therefore be excluded for those cases. While phenotype matching has been demonstrated in a large range of species

Table 1: Predictors of actor responses to visual stimuli during behavioral tests (LMM). Degrees of freedom (DF), *F*-statistic and p-values are provided (*F*, p). Significant predictors ($p < 0.05$) are shown in bold and trends ($p < 0.10$) in italics

		All pairs (n = 39 tests)		Unfamiliar pairs (n = 22 tests)	
Predictors		Approach time	Bouts of interest	Approach time	Bouts of interest
Pair	Familiarity	1.12, 0.30	0.35, 0.56	–	–
	Relatedness	0.24, 0.63	**5.43, 0.026**	**5.10, 0.036**	2.96, 0.10
Interaction	Relatedness × actor age	–	*4.01, 0.053*	–	–
	Relatedness × donor age	–	*3.04, 0.090*	–	–
	Relatedness × donor sex	–	–	**6.66, 0.018**	–
	Actor sex × donor sex	–	–	**5.39, 0.032**	**6.35, 0.020**
Actor	Age	2.28, 0.14	*3.82, 0.059*	**9.57, 0.006**	*3.24, 0.087*
	Sex	0.01, 0.91	0.30, 0.59	**6.26, 0.022**	**10.74, 0.004**
	Number of tests	**4.50, 0.041**	1.01, 0.32	0.50, 0.49	0.28, 0.60
Donor	Age	0.06, 0.80	**5.83, 0.021**	1.78, 0.20	**8.4, 0.009**
	Sex	0, 0.98	*3.41, 0.074*	1.58, 0.22	**5.36, 0.031**

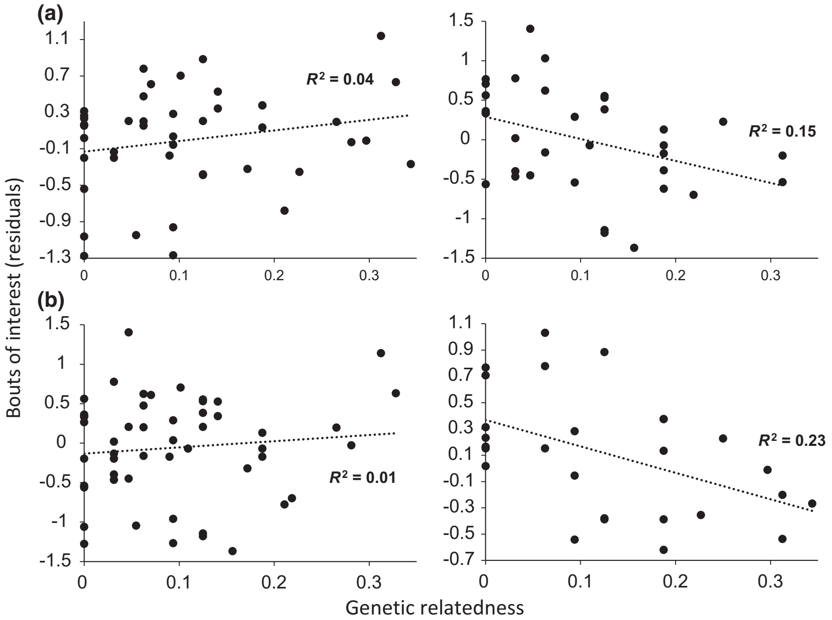

Fig. 1: Behavior of interest and actor–donor genetic relatedness. (a) In two age classes of actors; (b) in two age classes of donors. For the sake of clarity, we considered two classes of actors and donors: those that were younger (left graphs) than the average and those that were older (right graphs) than the average (in actors: mean age = 15.0 yr; in donors: mean age = 12.2 yr). The graphs represent the residuals of the total number of bouts of interest exhibited by actors toward visual stimuli as a function of actor–donor genetic relatedness. Residuals were obtained from a regression that included the other predictors of the relationship (see Table 1). The regression line as well as the percentage of variance explained are provided.

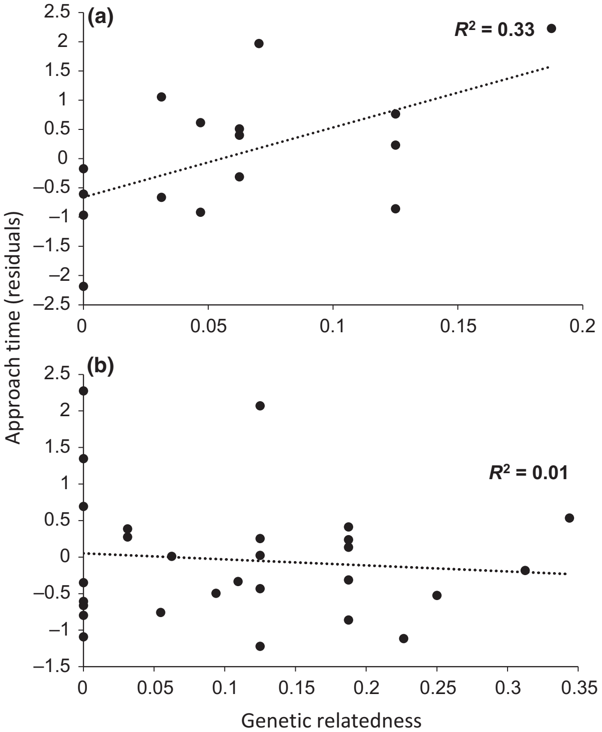

Fig. 2: Approach time spent and actor–donor genetic relatedness, during behavioral tests performed (a) on unfamiliar male–male donors and, (b) on unfamiliar female–female donors. The graphs represent the residuals of the total time of approach displayed by the actors toward stimuli as a function of actor–donor genetic relatedness. Residuals are obtained from a regression that included the other predictors of the relationship (see Table 1). The regression lines as well as the percentage of variance explained are provided.

(e.g., in insects: Fischer et al. 2015; Lihoreau et al. 2007; fishes: Barbosa et al. 2016; Hesse et al. 2012; Thuenken et al. 2014; rodents: Mateo 2003), such experiments have rarely been conducted with primates because the confounding effects of learning direct familiarity are often difficult to disentangle from those due to the learning of common phenotypic templates. Indeed, most primates live in large, permanently bisexual groups where numerous kin are available to familiarize with. Consequently, in such social settings, carefully controlled experimental designs are required to unambiguously test the phenotype matching hypothesis.

Such experiments are, however, difficult to perform in natural environments. Yet, in studies on free-ranging rhesus macaques, male migration patterns allowed to eliminate most (if not all) of the confounding effects of direct familiarity: During behavioral tests, individuals not raised in the same social group discriminated both the voices (Pfefferle et al. 2013) and faces (Pfefferle et al. 2014) of their paternal half-sibs in comparison with non-kin. However, some forms of indirect familiarity among study subjects were impossible to rule out completely because intergroup encounters are frequent on the island. In our study group of mandrills, we already unambiguously demonstrated phenotype matching as a mechanism of acoustic kin discrimination (Levréro et al. 2015). Indeed, the auditory channel of communication encodes information about genetic relatedness between callers and receivers: Vocalizations of relatives are structurally more similar to each other than are those of unrelated animals. Moreover, as for facial traits, mandrills can discriminate their unfamiliar relatives based on these vocal cues alone (Levréro et al. 2015). Such redundant or ‘backup’ (Johnstone 1996) cues of relatedness may have arisen because coding (or decoding) the information contained in phenotypic traits is imperfect. Redundant cues are found in a large array of species, in multiple sociosexual contexts. They allow different components to provide the same information to improve the accuracy of receiver response (see, for review, Rowe 1999; Hebets & Papaj 2005). While acoustic communication in mandrills may serve to transmit information over longer distances, visual cues may reinforce this information at shorter distances. Combining several phenotypic traits during behavioral tests might allow testing for potential increased accuracy of receiver responses or the relative importance of different modalities in future studies.

In the present study, we found contrasting results according to the type of behavioral responses considered. While actors approached the pictures of unfamiliar related male donors for longer periods of time, suggesting a possible absence of anxiety in proximity of kin, they investigated the pictures of less related donors more, suggesting an increased interest in genetically distant conspecifics, as also shown by rhesus macaques (Pfefferle et al. 2014). ‘Passive’ proximity could be regarded here as a by-product if more ‘active’ behavior of interest displayed toward a given picture involves an automatic decrease in the time spent in proximity of the paired picture. This is, however, improbable because we would have observed a negative relationship between our two predictors, which was not the case: When actors spend more time in proximity of a given picture, they also tend to investigate it more often ($R^2 = 36\%$; regardless of the degree of relatedness between actors and donors).

Finally, most of the effects reported here were found in combination with both actor and donor characteristics. While experimental sessions involving presentation of stimuli from same-sex pairs generally produced more pronounced behavioral responses, both male and female actors spent more time in proximity of pictures of related, unfamiliar male donors (the strongest effect we found overall). Contrary to rhesus macaques, where relatives elicited more interest than non-kin when donors were of the same sex as actors (Pfefferle et al. 2014), male mandrills appear not to present a strong threat to other males, as proposed in the macaque study. In mandrills, females are philopatric and may therefore interact with relatives throughout their lives. In contrast, male mandrills disperse as early as 6 years of age from their natal group (Abernethy et al. 2002), so that males are the more unfamiliar sex.

Phenotype matching mechanisms are expected to evolve when direct familiarity is hampered and our results partly corroborate this notion. Additionally, behavioral interest elicited by relatives tended to be greater in older actors, and pictures collected from older donors also tended to provoke more interest than younger animals. In line with those results, older macaque actors tended to look more at kin images compared to younger animals (Pfefferle et al. 2014). In humans, kin detection abilities in unfamiliar third parties are already present at 5 years of age but is better in young adolescents of 11 years (Kaminski et al. 2012). However, the age-biased response we report in mandrills is probably due to social experience and skills individuals acquire throughout their life rather than maturational cognitive processes because all tested mandrill actors were fully grown adults. Alternatively, older animals may have more interest in recognizing their relatives than younger ones and/or juveniles are not yet interested in visual representations of potential mates lowering their interest toward such stimuli. Finally, further morphological studies during individuals’ development are now required to test whether cues of relatedness are more pronounced as individuals aged, as our behavioral tests seem to suggest.

Overall, our results provide additional evidence that behavioral biases among unfamiliar kin have evolved through kin selection processes. If several proximate mechanisms exist to detect these unfamiliar kin, the underlying selective pressures may have been substantial. Additionally, in mandrills, new encounters in dense and closed habitats may hamper accurate evaluation of phenotypic cues possibly leading to the evolution of backup signaling in this species. Large group sizes and dense habitats are two prominent characteristics of mandrill’s ecology (Abernethy et al. 2002). Selection for discriminating unfamiliar kin, and more generally for discriminating among individuals, is probably higher in species forming large groups where numerous potential sociosexual partners are available to interact with. In line with this notion, social group size in sciurid rodents has promoted the evolution of more pronounced individual signatures in alarm calls to facilitate individual discrimination (Pollard & Blumstein 2011). In humans, faces show elevated phenotypic variation and lower between-trait correlations compared to any other traits (Sheehan & Nachman 2014). Discriminating among individuals therefore appears to be a critical social ability found in a wide range of animal taxa.

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Supporting Information

Additional supporting information may be found in the online version of this article at the publisher’s web-site:

Figure S1: Three examples of pictures (donors) used during the behavioral tests performed.

Figure S2: Raw data.