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ORIGINAL ARTICLE

Rhesus macaques (*Macaca mulatta*) recognize group membership via olfactory cues alone

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Abstract The ability to distinguish group members from conspecifics living in other groups is crucial for gregarious species. Olfaction is known to play a major role in group recognition and territorial defense in a wide range of mammalian taxa. Although primates have been typically regarded as *microsmatic* (having a poor sense of smell), increasing evidence suggests that olfaction may play a greater role in primates' social life than previously assumed. In this study, we carried out behavioral bioassays using a signaler-receiver paradigm to investigate whether rhesus macaques (*Macaca mulatta*) can discriminate between body odors of female group members and females from different social groups. We conducted the study on the research island Cayo Santiago, Puerto Rico, in the non-mating season and controlled for kinship and familiarity using extensive pedigree and demographic data. Our results indicate that both males and females inspect out-group odors significantly longer than in-group odors. Males licked odors more often than females, and older animals licked more often than younger ones. Furthermore, individuals tended to place their nose longer towards odors when the odor donor's group rank was higher than the rank of their own group. Reuse of odor samples decreased odor intensity (rated by human experimenters) during the course of a given test day and with longer exposure to ambient air; however, the reuse of odor samples did not significantly influence the response behaviors. Our findings uncover key roles of olfactory communication in a species not possessing distinct scent glands and thus shed light into the evolution of primate olfactory communication.

Keywords Olfactory communication · Rhesus macaques · Bioassay · Group recognition · Individual recognition · Familiarity

Introduction

For gregarious species, the ability to distinguish group members (in-group individuals) from conspecifics living in other groups (out-group individuals) is of crucial importance as it allows individuals of the same group to protect resources such as food, mating partners, or sleeping sites against intruders while ensuring social cohesion within the group. In addition to visual (domestic cattle, Coulon et al. 2010; Barbary

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macaques, Schell et al. 2011) and acoustic (elephants, McComb et al. 2000; chimpanzees, Herbinger et al. 2009; horses, Lemasson et al. 2009; dolphins, Quick and Janik 2012) cues, olfaction plays a major role in group recognition and territorial defense in a wide range of taxa (reviewed, for mammals, in Tang Halpin 1986). For example, black-tailed deer (*Odocoileus hemionus columbianus*, Müller-Schwarze 1971), African dwarf mongoose (*Helogale undulata rufula*, Rasa 1973), and Mongolian gerbils (*Meriones unguiculatus*, Tang Halpin 1976) treat familiar individuals and strangers differently, discriminating between them using olfactory cues. Domestic dogs (Dunbar and Carmichael 1981), horses (*Equus caballus*, Péron et al. 2014), and Columbian ground squirrels (*Spermophilus columbianus*, Harris and Murie 1982) also discriminate between in-group and out-group individuals, spending more time investigating odors from unfamiliar conspecifics as compared to odors from group or colony members.

In primates, however, the role of olfaction is far less understood than in other mammalian species, most likely because primates were typically regarded as *microsmatic*, relying more on visual and acoustic rather than on olfactory information. The olfactory bulbs and olfactory epithelia are proportionately smaller in primates compared to most other mammals (Baron et al. 1983; Smith and Bhatnagar 2004), and among primates, the ratio between total brain volume and olfactory bulb volume decreases from strepsirrhines to anthropoids (Stephan et al. 1970). Despite the anatomical evidence for a relative reduction in olfactory structures during primate evolution, it is currently debated whether this corresponds to a functional reduction in olfactory abilities of Old World monkeys. In fact, a growing body of evidence suggests that olfactory communication may play a significant role in the regulation of a wide range of primate behaviors (Heymann 2006; Drea 2015). Strepsirrhines and New World monkeys, in particular, appear to have well-developed olfactory capabilities with odor cues indicating reproductive state, dominance rank, individual identity, and even genetic information which can be perceived by the animals (e.g., cotton-top tamarins, *Saguinus oedipus*, Ziegler et al. 1993; common marmosets, *Callithrix jacchus*, Smith et al. 1997; ring-tailed lemurs, *Lemur catta*, Palagi and Dapporto 2006; Scordato and Drea 2007; Charpentier et al. 2008; Charpentier et al. 2010).

In contrast, very little is known about the olfactory capabilities of Old World monkeys and apes, although recent evidence indicates that, in these taxa, chemical communication plays an important role as well. Most evidence until now has come from species which perform classical scent marking and/or have specific glands used for olfactory communication. Mandrills (*Mandrillus sphinx*), for example, signal both variable (age and, in males, dominance rank) and fixed (sex and, possibly, individual identity) information in their odor profiles (Setchell et al. 2010). They show morphological (nasopalatine ducts) as well as behavioral (flehmen) traits usually associated with the processing of non-volatile odorants by the vomeronasal organ (Charpentier et al. 2013). Furthermore, western lowland gorillas (*Gorilla gorilla gorilla*) are able to discriminate between different odors such as almond and vanilla (Hepper and Wells 2012) and produce individual body odors which can be identified by human raters (Hepper and Wells 2010).

In order to fully assess the importance of olfactory communication in the primate order and to shed light on its evolution, it is essential to consider catarrhine species without distinct scent glands and scent-marking behavior as well. There is very limited information on olfactory behavior in species which lack these features (chimpanzees, *Pan troglodytes*, Mitani and Watts 2005; Herbinger et al. 2009; chacma baboons, *Papio hamadryas ursinus*, Clarke et al. 2009). Rhesus macaques (*Macaca mulatta*) represent an ideal model species as they have been observed to use olfaction in a variety of contexts, although they do not seem to possess scent glands and do not perform scent marking (Geissmann 1987). They inspect food via smelling and sniff various body parts including the head or anus of conspecifics, and males sniff females' genitals, especially during the mating season (SH, personal observation). Rhesus macaques on Cayo Santiago were recently observed to exhibit exploratory behavior, including smelling, towards the body of a dead and heavily injured monkey (Buhl et al. 2012), possibly to gain information about its individual identity or group membership. Furthermore, as rhesus macaques are considered to be a highly despotic species demonstrating high levels of intra- and intergroup aggression (Loy 1970; Boelkins and Wilson 1972; Flack and de Waal 2004), they are ideal to study the mechanisms of group recognition in primates.

While visual cues appear to be well suited for individual or group recognition during daytime (Pokorny and de Waal 2009; Schell et al. 2011), olfactory cues pertaining to group membership are also available at night. Nocturnal primates are known to rely heavily on their olfactory sense. Owl monkeys (*Aotus nancymaae*), for example, are able to recognize sex, age, and family membership via olfactory cues (MacDonald et al. 2008). Nocturnal activity including moving, vocalizing, feeding, or even playing has also been described for several diurnal primate species (gelada baboons, *Theropithecus gelada*, Kawai and Iwamoto 1979; Japanese macaques, Nishikawa and Mochida 2010; ring-tailed lemurs, Donati et al. 2013; Guizhou snub-nosed monkeys, *Rhinopithecus brelichi*, Tan et al. 2013; chimpanzees, Zamma 2014; Krief et al. 2014) including rhesus macaques (Vessey 1973). Thus, olfactory signals and body odor may play an important role when it comes to territorial defense and group cohesion at night. Furthermore, in contrast to acoustic and visual cues, olfaction has a long-lasting effect in communication. Odors conveyed through urine, feces, body secretions, or fur can be perceived for a longer time even if the individual is not present any more. Thus, odor may be important for rhesus macaques as a long-lasting signal disclosing group membership.

In the present study, we conducted behavioral bioassays under natural conditions to investigate whether rhesus macaques are able to discriminate between odors of unrelated, familiar group members and unrelated, unfamiliar individuals belonging to a different social group. Using an experimental, signaler-receiver paradigm, we presented recipients (hereafter, test subjects) with body odors from either in-group or out-group individuals (hereafter odor donors). As previous studies suggest that rhesus monkeys behaviorally differentiate between kin and non-kin in several social contexts (Widdig 2002; Widdig et al. 2001, 2006a, b) and, as olfaction, apart from visual and acoustic cues (Pfefferle et al. 2014a, b), might constitute a likely mechanism for kin recognition, we excluded the potential effect of kinship on odor discrimination using only dyads that are unrelated up to the grandparent generation. Furthermore, since males might be, in general, more familiar to conspecifics outside their current group than females because, in contrast to females, they change groups several times throughout their lives (Colvin 1983; Gouzoules and Gouzoules 1987), we aimed to control for a potential effect of familiarity in the out-group condition by testing only dyads that never lived a single day together in the same group. Cayo Santiago is a suitable study site for our experiments as extensive pedigree as well as demographic data are available which allow controlling for both kinship and familiarity. Given that unfamiliar stimuli are known to provoke greater interest than familiar ones in a number of taxa as outlined above (e.g., Dunbar and Carmichael 1981; Harris and Murie 1982; Péron et al. 2014), we expected rhesus macaques to show stronger behavioral responses towards the odor of out-group as compared to in-group individuals. Finally, we conducted our study in the non-mating season to avoid potential influences of hormonal changes on the test subjects' response behaviors. As female rhesus macaques are the philopatric sex (Gouzoules and Gouzoules 1987) and the most active part when defending food resources (Koford 1963; Hausfater 1972), we expected females to respond stronger towards out-group odors than males in a non-mating context.

Materials and methods

Study species and population

This study was conducted on semi-free-ranging rhesus macaques living in Cayo Santiago, a 15.2-ha island offshore of Puerto Rico managed by the Caribbean Primate Research Center (CPRC). Rhesus macaques live in multi-male, multi-female groups characterized by female philopatry (Gouzoules and Gouzoules 1987) and male dispersal (Lindburg 1969; Colvin 1983). Females typically remain in their natal groups throughout their lives and form stable dominance hierarchies according to their matrilineal kinship, while males emigrate from their natal groups at the onset of puberty and may transfer groups throughout their lives in search of mating opportunities (Melnick et al. 1984; Rawlins and Kessler 1986). Rhesus macaques are seasonal breeders (Drickamer 1974) and mate highly promiscuous, with inter-birth intervals of approximately 1 year (Rawlins and Kessler 1986). The mating season in Cayo Santiago lasted from March to August followed by the birth season from September to February (Hoffman et al. 2008).

During the study period from September to December 2011, Cayo Santiago was inhabited by approximately 1150 individuals which are all direct descendants of the 409 founder animals introduced from India in 1938 (Rawlins and Kessler 1986). Although no individual has ever been added to the population except via natural births, pedigree analyses suggest that this population is not inbred (Widdig et al. 2004). All subjects were habituated to human observers and could be individually identified. At the beginning of the study, the population comprised six social groups with group sizes that are representative of those of wild rhesus macaques which vary widely between 10 and 240 individuals (Seth and Seth 1986; Southwick et al. 1996). Group sizes were the following (mean±SD): groups F=313±22, R=257±16, HH=149±10, V=144±11, KK=142±7, and S=108±5. The dominance between groups can be established based on the retreat of one group when another group is approaching or challenging, usually seen at feeding sites, or as the outcome of aggressive intergroup encounters. Based on daily observations by CPRC census takers, groups ranked as follows: F>R>KK>V>HH>S.

Given that the population has been studied extensively, a large amount of information exists regarding their intergroup behaviors and interactions. Individuals of one group tend to travel cohesively several times a day, especially when moving towards feeding areas (Boelkins and Wilson 1972). Groups are not restricted to a special area on the island (Carpenter 1942); nevertheless, each group has a distinct home range in which it typically moves, with ranging areas of different groups overlapping to some extent, especially around feeding areas. These feeding areas are, thus, typically the places where most of the intergroup conflicts occur (Kaufmann 1967). Intergroup encounters are mostly aggressive, although only about 9 % of the cases involve physical violence (Boelkins and Wilson 1972).

Although the macaques forage up to 49 % on the natural vegetation found in Cayo Santiago (e.g., foliage, fruits, insects, and soil; Marriott et al. 1989), they are provisioned daily with commercial monkey chow as main food (Teklad NIB Primate Diet 8773; Teklad Harlan, Madison, WI, USA). Thus, the influence of diet on the variation in individual body odors should be limited.

Odor sample collection

Body odor samples from 70 individuals selected for other ongoing projects were collected by SH during the annual trapping season conducted by the CPRC from January to March 2011 before the onset of the mating season. Prior to sampling, cotton swabs were prewashed in 99 % methanol and 99 % pentane for 6 h each to remove any volatile compounds naturally occurring in the cotton and stored in airtight and pre-cleaned 4-ml chromatography vials (see Charpentier et al. 2008).

As part of the trapping procedure, animals were anesthetized by CPRC veterinarians using an intramuscular injection of ketamine (10 mg/kg body weight) after being captured. While one study suggests that cortisol levels rise after ketamine administration (Puri et al. 1981), others show that ketamine has no effect on stress levels in rhesus macaques (Fuller et al. 1984; Bentson et al. 2003) or, if so, cortisol levels rose only 2 h after ketamine injections (Wickings and Nieschlag 1980). Nevertheless, sample collection was performed within 30 min of anesthetization to minimize the possible influence of ketamine and stress on the body odor.

To obtain body odor samples, swabs were repeatedly rubbed with sterile forceps against the genital region for 20 s and stored in the vials at −20 °C on the island until transferred to −80 °C immediately after return to the laboratory on the mainland of Puerto Rico using a transportable cooling bag (cf. Scordato et al. 2007; Lenochova et al. 2008). Seven genital samples per individual were collected, leading to a total of 490 samples.

Assessment of relatedness

To exclude a potential effect of kinship on odor recognition, only individuals that were assigned as unrelated to the odor donor were included in the bioassay. To do so, we took advantage of the extensive genetic database of the Cayo Santiago population, started in 1992, which includes 4641 animals, to date, genotyped for an average of 27.6±1.6 loci (mean±SD, details in Widdig et al., under review). We selected all genotyped animals alive during the study and identified individuals (potential test subjects) which are maternally and paternally unrelated up to the grandparent generation with respect to 1 of the 70 odor donors. In other words, we chose individuals of genetically determined maternity and paternity and, to increase our kinship information, we aimed to assign maternal and paternal grandfathers, too. The criteria of established maternity and paternity in this database have been explained elsewhere (Widdig et al., under review). We then used a pedigree-based approach, based on the above parentage assignments, to detect dyads unrelated for at least two generations (shared neither parents nor grandparents, respectively; hereafter, non-kin). Thereby, we were able to exclude relatedness via the maternal and paternal line up to the grandparent generation for the 104 dyads used in our test.

Assessment of familiarity

Given that males, in contrast to females, change groups several times throughout their lives (Colvin 1983; Gouzoules and Gouzoules 1987), we aimed to control for the impact of familiarity in the out-group condition. We used co-residence (number of days the test ID lived in the same group as the odor ID) as an estimate of how familiar two individuals might have been. Co-residence was determined based on demographic data provided by the CPRC including group membership and migration events. For the out-group condition, we only used dyads that never lived a single day together in the same group (hereafter, unfamiliar). Familiar individuals (living in the same group) had a co-residence of at least 221 days in the same group (mean±SD=1786±671.67 days, range=221–4722 days).

Behavioral bioassays

Study period and design

Bioassays were conducted during the non-mating season from September to December 2011 to avoid any influence of hormonal changes on behavioral responses of the test subjects. Odor samples were presented in metal tea eggs (4×2.5 cm) with additional drilled holes and attached to a 5-m-long string (1 mm in diameter, Fig. 1). Tea eggs were chosen as an ideal apparatus for odor presentation in the field since they do not exhibit an inherent smell and could be easily cleaned with 95 % ethanol. Odor samples of 33 different females (age range=7–22 years, mean±SD=9.06±3.54) out of 5 groups (F, R, KK, HH, and S) were presented to a total of 74 individuals of both sexes (39 females and 35 males). We only chose female odor donors because, firstly, due to the reliance on individuals selected for ongoing projects during the trapping procedure, there were many more female odor samples available compared to male ones and, secondly, we wanted to avoid introducing another variable (sex of odor ID) in the already complex statistical model. Two of the odor donors were also used as test subjects (see Online Resource 1). Only adult individuals were tested (males: age range=4–15 years, mean±SD=5.83±2.49; females: 4–22 years, mean±SD=6.13±3.33).

A pilot study conducted by SH in spring 2011 in which two tea eggs were simultaneously presented revealed that olfactory behavior towards both tea eggs was shown in only 13 % of all trials (*N*=67), whereas in 57 % of the trials, only one tea egg was investigated (in 30 %, they ignored the tea egg; SH, unpublished data); thus, to increase the probability of successful trials and due to limited odor samples, a presentation of one tea egg at a given time was chosen for the bioassays presented here.

We used a combined approach of a within- and between-subjects design where each test subject was presented with (a) a familiar non-kin odor (in-group condition) and/or (b) an

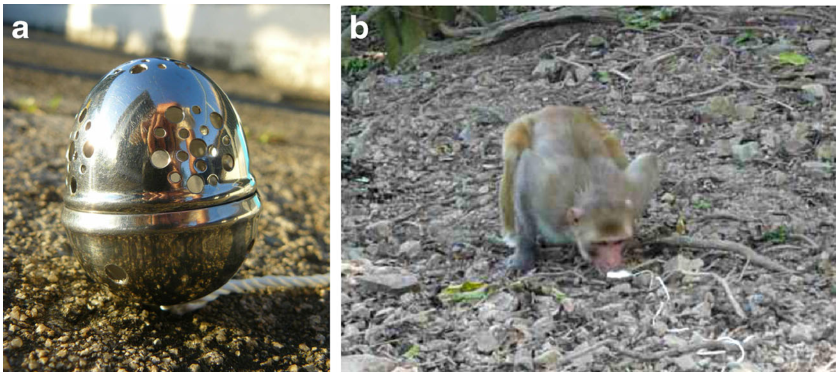

Fig. 1 **a** Test apparatus used for presenting odor samples during the behavioral bioassay. Five odor samples of a respective individual (all collected on the same day within 5 min) were pooled in one tea egg to increase odor intensity. **b** Male rhesus macaque sniffing at the test apparatus including odor samples of an out-group female

unfamiliar non-kin odor (out-group condition). Thirty individuals (18 females and 12 males) were tested in both conditions, and another 44 individuals (21 females and 23 males) were tested in only one condition due to the reluctance of some subjects to participate twice. For test subjects that were tested twice, the order of the stimuli presented was counterbalanced and randomized. The same number of test subjects was first presented with the in-group (N=15) or the out-group (N=15) odor, respectively. Likewise, for test subjects that were only tested once, the number of trials tested for each condition and sex was balanced. To reduce the potential effect of habituation, trials of the two different test conditions for a given animal were conducted at least 4 days apart (range=4–51 days, mean±SD=17.83±14.27 days).

A trial was defined as olfactory trial when a test subject showed olfactory behavior towards the tea egg (sniff, grab-sniff, hand-sniff, lick, touch-lick, or nose within 15 cm; for definitions, see Table 2). Non-olfactory trials were defined as the test subject approaching the tea egg within 1 m but not directing attention to it (e.g., passing by) or the test subject directing attention to the tea egg without showing olfactory behavior (e.g., pause, gaze at, handle). Only olfactory trials were used for statistical analysis (N=104). While conducting the bioassay, attention was paid to ensure that the number of olfactory trials was approximately balanced for the two test conditions, sex and group (Table 1).

Preparation for the bioassays

For each odor donor, a dyad list of all unrelated test subjects was used in the field in order to find appropriate test subjects and ensure optimal testing. Whenever odor samples were going to be used on a given day, they were put on ice in a cooling bag when transported to the field site. Samples of not more than 5 odor donors were taken to the field per day in order to avoid unnecessary thawing of unused samples. Prior to each trial, five cotton balls per odor donor were thawed for approximately 1–2 min and pooled in one tea egg in order to increase odor intensity; after each trial, samples were immediately put back on ice and the time the samples have been exposed to ambient air was noted down. Samples were handled with clean forceps at all times and were reused as it has been previously demonstrated that freezing does not affect sample quality even if samples are thawed repeatedly (Lenochova et al. 2008; Roberts et al. 2008). Overall, 26 of the 33 odor sample sets were used more than once (two to seven times). As humans were shown to be successful raters of catarrhine primates' odor (Laska and Freyer 1997; Hepper and Wells 2012), two persons independently rated the strength of the odor samples used per bioassay once at the beginning and once at the end (approximately 8 h later) of a given test day to get an estimate of odor intensity. The raters assigned a score from 0 (no smell) to 10 (very strong smell) to the odor samples. As soon as one rater allocated an intensity score of less than 2, odor samples of the respective odor donor were omitted from further use. Until use, tea eggs were kept in clean ziplock bags, which were labeled with odor donor ID, and were always carefully handled in these bags without touching them to avoid contamination by human body odors; no gloves were used since latex gloves were revealed to transfer an unwanted smell on the tea eggs.

Table 1 Overview of the number of tested individuals per test condition (in-group/out-group), group, and sex in the olfactory in-group/out-group bioassay

Test condition	Group	Female	Male	Total
In-group	F	6	6	12
	HH	4	3	7
	KK	3	1	4
	R	13	6	19
	S	3	3	6
In-group total		29	19	48
Out-group	F	4	7	11
	HH	2	3	5
	KK	4	5	9
	R	14	8	22
	S	4	5	9
Out-group total		28	28	56
Total		57	47	104

Conducting the bioassay

Test subjects were randomly chosen. Once a potential test subject was located in the field, the tea egg containing the respective odor donor samples was placed on the ground in front of the test subject at a distance of approximately 2 m. The behavior of the test subject was recorded with a digital video camera (Panasonic HDC-SD40) set approximately 5 m in front of the individual. In order to make test trials comparable, every effort was made to find test subjects in equal conditions. The animal could be tested if it was awake but not engaged in grooming (except self-grooming) or feeding activity, undisturbed by any surrounding activity or noise; if no major activity was happening within the rest of the group (e.g., a fight or group travel); and if no other animals were within 2 m of the test subject. If other animals were within 2 m, they were ranked lower than the test subject. In addition, times of day as well as predominant weather conditions were aimed to match between trials. When conducting the trials, adverse weather conditions, such as heavy rain and strong winds, were avoided.

Two experimenters carried out the bioassay (SH as presenter and one camera person). The presenter of the odor stimuli was blind towards the test condition presented, and the camera person was choosing the odor samples for each test trial. Video recording was finished as soon as the test subject left the 5-m radius around the tea egg or after 5 min if the animal stayed within the 5-m radius. When the tea egg had been touched by an animal, the samples were immediately put back on ice and a new, clean tea egg was used for the next trial to avoid the potential influence of the previous animal's body odor on the tea egg.

Video analysis and behavioral definitions

The behavioral responses of the test subjects in olfactory trials were analyzed frame-by-frame using Mangold Interact version 8.4.7 (see Online Resources 2 and 3 for video examples). Analysis started with the first olfactory behavior shown by the test subject. The duration and the number of all olfactory behaviors were recorded. In order to get an insight of how attracted the subject was towards the respective odor (following the approach by Munakata et al. 2001), the duration of the following subsequent behaviors was coded: presence of the animal within 2 m from the tea egg, handling, touching, or looking at the tea egg. Self-scratching was recorded as a measure of nervousness as it is known that this type of self-directed behavior constitutes a coping mechanism towards stress (Maestripieri et al. 1992; Maestripieri 1993; Castles et al. 1999; Gustison et al. 2012). Videos were analyzed by one rater, and in order to estimate inter-observer reliability, a subset of videos (N=20, 15.9 %) was analyzed by the second rater. Both raters were blind to the test condition per trial. Inter-observer reliability was estimated using Spearman's rank correlations on the durations for each behavior of the two datasets (Martin and Bateson 1993), revealing always highly significant correlations (N=20, r_s=0.74–1.0, mean of r_s=0.94, P<0.001).

Statistical analysis

Effect of odor sample reuse on odor intensity

First of all, we tested whether the reuse of odor samples over the course of the study as well as during a given test day had an effect on odor intensity using a general linear mixed model (GLMM; Baayen 2008). We found that intensity scores significantly decreased from the beginning (pre) to the end (post) of a given test day [N=305, estimate=1.077, standard error (SE)=0.291, χ^2=4.851, degree of freedom (df)=1, P=0.028] and that the total time the odor samples have been exposed to ambient air up to a given test trial tended to have a negative effect on intensity scores (N=305, estimate=−0.486, SE=0.259, χ^2=3.420, df=1, P=0.064). Further details on the analysis are provided in Online Resource 4. We used ambient air time as a control variable for subsequent analysis.

Response behaviors towards in-group and out-group odors

Prior to testing whether rhesus macaques showed a different behavioral response towards the odor of in-group or out-group conspecifics, respectively, the previously separated olfactory behaviors sniff and grab-sniff were combined to *sniffing* as well as lick and grab-lick to *licking* since we expected the monkeys to perceive the same olfactory information from them; likewise, we combined handle and touch to *handling* (Table 2). We did not include hand-sniff to sniffing as we did not expect the monkeys to perceive equally direct olfactory information as compared with sniff and grab-sniff. As it only occurred in three cases, we excluded hand-sniff from further analysis. Furthermore, since the response variables looking and time spent within 2 m were highly correlated (Spearman correlation: r_s=0.70, S=60383.45, P<0.001), we ran a principal component analysis (PCA) to get a composite measure of these two variables using the function "prcomp" (with the arguments *scale* and *center* set to *true*) in R (R Core Team 2015). The PCA revealed one PC with an eigenvalue ≥1 explaining 87 % of the total variance. Loadings on PC1 were 0.71 for both looking and time spent within 2 m. PC1 was used as a response variable for further analysis.

In order to test whether rhesus macaques showed a different behavioral response towards the odor of in-group or out-group conspecifics, respectively, we used GLMMs with Gaussian error structure and identity link for the response variables nose within 15 cm, sniffing, handling, and PC1, respectively. We visually checked the response variables for

Table 2 Definitions of behaviors shown during the olfactory in-group/out-group bioassay in the present study

Behavior	Definition
Sniff	Moving the nose towards the tea egg up to a distance of ≤3 cm
Grab-sniff	Grabbing the tea egg and moving it towards the nose up to a distance of ≤3 cm
Hand-sniff	Touching the tea egg by hand and instantaneously moving the hand to the nose up to a distance of ≤3 cm. The animal does not walk on its hand between touching the tea egg and sniffing the hand
Lick/bite	Touching the tea egg by tongue or biting into the tea egg
Grab-lick/bite	Taking the tea egg to the mouth and touching it by tongue or biting into it
Nose within 15 cm	Nose is directed towards the tea egg within a distance of ≤15 cm, while the animal pays active attention towards the tea egg
Time spent within 2 m	Time spent within 2 m of the tea egg after the animal has shown the first olfactory behavior. The animal can sit, stand, lie, or move within the 2 m. Time spent within 2 m can occur with any other behavior simultaneously
Touch	Briefly touching the tea egg without lifting it
Handle	Grasping or lifting the tea egg. Can also include lifting or moving the egg at the string but does not include handling the string alone without moving the tea egg
Looking	Gazing at the tea egg within an angle of 15° without any other behavior occurring. The animal is paying direct attention to the tea egg
Self-scratch	The animal scratches parts of its body

their distribution and log-transformed them where necessary (sniffing, nose within 15 cm, handling) to obtain approximately symmetric distributions. Since the variables licking and self-scratch usually lasted for very short durations and self-scratch was rare, we analyzed the counts of these variables using generalized linear mixed models with Poisson error structure and log-link function. In order to test whether the subjects' responses varied depending on the relative group rank of the odor donor to their own group rank, we created a vector for group rank difference (the group rank of test subject−the group rank of odor donor) where higher values indicated higher rank differences (positive values mean that the test subject was confronted with an odor donor of a lower-ranking group, and negative values mean that the test subject was confronted with an odor donor of a higher-ranking group).

A GLMM was run for each response variable (sniffing, nose within 15 cm, handling, PC1, licking, and self-scratch) separately into which we included test condition (in-group/out-group), sex and age (in days) of the test subject, group rank difference, as well as ambient air time as fixed effects and test subject ID, odor donor ID, group of test subject ID, and group of odor donor ID as random effects. Random slopes (Schielzeth and Forstmeier 2009; Barr et al. 2013) within the group of test subject ID or group of odor donor ID were included for sex, test condition, and group rank difference. Within odor donor ID or test subject ID, random slopes were not included since only few odor donor IDs and no test subjects were tested more than three times and, thus, random slopes were not estimable for a reasonable number of levels of these random effects (Barr et al. 2013). Since we assumed that the males might react differently towards female out-group odors than females, we also included the interaction between test condition and sex into the model. Prior to running the model, we *z* transformed the predictor variables test subject age, group rank difference, and ambient air time to a mean of zero and a standard deviation of 1 to get easier interpretable estimates (Schielzeth 2010). To check for the assumptions of normally distributed and homogeneous residuals for models with Gaussian error structure (for the response variables nose within 15 cm, sniffing, handling, and PC1), we visually inspected qqplots and scatter plots of the residuals plotted against fitted values. These did not indicate any obvious violations of these assumptions. In the case of models with Poisson error, overdispersion was not an issue neither for licking (dispersion parameter=0.232, $\chi^2=22.762$, $df=98$, $P=1$) nor for self-scratch (dispersion parameter=0.259, $\chi^2=25.171$, $df=97$, $P=1$). We checked for model stability by excluding the levels of the random effects one at a time from the data and comparing the estimates derived with those obtained for the model based on all data, which indicated no influential cases to exist. Variance inflation factors (VIFs, Field 2009), derived from the function "vif" of the R package "car" (Fox and Weisberg 2011) applied to a standard linear model excluding the random effects and the interaction, revealed no collinearity issue (max VIF=3.265, mean VIF=1.819). The significance of the full model as compared to the null model (comprising test subject age, group rank difference, ambient air time, random effects, and random slopes, Forstmeier and Schielzeth 2011) was established using a likelihood ratio test (LRT, Dobson 2002, R function *ANOVA* with argument *test* set to "Chisq"). To achieve a more reliable *P* value, we fitted the model using maximum likelihood (rather than restricted maximum likelihood; Bolker et al. 2009). *P* values for the individual effects were based on LRTs comparing the full model with a respective reduced model lacking the particular predictor to be tested (Barr et al. 2013). The models with Gaussian error structure were fitted using the function "lmer" of the R package "lme4" (version 1.1-8, Bates et al. 2015). For the response variables with Poisson error structure, the models were fitted using the function "glmer" of the R package "lme4".

Effect of familiarity on response behaviors

Finally, in order to test whether the level of familiarity in the in-group condition influenced the response behavior of the test subjects, we ran an additional GLMM for each response variable whose full-null model comparison was significant in the original model. We included co-residence and all previously significant predictor variables as fixed effects as well as odor ID, group of odor ID, and group of test ID as random effects. Random slopes within the random effects were included where possible (for nose within 15 cm, random slopes of co-residence within group of test subject ID and group of odor donor ID; for licking, random slopes of co-residence and sex within group of test subject ID and group of odor donor ID). All other procedures equaled those outlined above.

Results

Response behaviors towards in-group and out-group odors

Our results revealed that the set of predictor variables used had a clear influence on the probability of the response variables nose within 15 cm (LRT comparing the fit of the full model with the fit of the null model containing test subject age, group rank difference, ambient air time, random effects, and random slopes: $\chi^2=9.994$, $df=3$, $P=0.019$) and licking ($\chi^2=10.007$, $df=3$, $P=0.019$). More specifically, the interaction between sex and test condition for both durations that the subjects placed their nose within 15 cm of the test odors (estimate=−0.46, SE=0.36, $\chi^2=1.60$, $df=1$, $P=0.205$) and licking (estimate=−1.053, SE=1.021, $\chi^2=-1.031$, $df=1$, $P=0.302$) was not significant. In order to obtain interpretable *P* values for the main effects, a reduced model not comprising the interaction for each response variable was run. For nose within 15 cm, the reduced model revealed a significant effect of test condition with test subjects showing a higher behavioral response towards out-group odors (Table 3, Fig. 2a). Furthermore, the higher the group rank of the odor donor in comparison to the rank of their own group, the longer the test subjects tended to place their nose towards an odor (Table 3, Fig. 3). Age and the time the odor samples have been exposed to ambient air did not have a significant effect on nose within 15 cm (Table 3).

Regarding the number of licking, the reduced model revealed a clearly significant effect of sex with males licking more often than females (Table 4, Fig. 2b). Furthermore, we found a significant positive effect of age on the number of licking with older subjects licking more often than younger subjects (Table 4). Condition, group rank difference, and ambient air time did not seem to have a significant effect on the number of licking (Table 4).

The set of predictor variables used did not appear to influence the probability of the response variables sniffing (LRT comparing the fit of the full model with the fit of the null model containing test subject age, group rank difference, random effects, and random slopes: $\chi^2=4.049$, $df=3$, $P=0.256$; Fig. 3), PC1 ($\chi^2=2.898$, $df=3$, $P=0.408$; Fig. 3), handling ($\chi^2=3.013$, $df=3$, $P=0.390$; Fig. 3), or self-scratch ($\chi^2=1.529$, $df=3$, $P=0.675$; Fig. 3). Thus, *P* values for the individual predictors were not interpreted.

Effect of familiarity on response behaviors

Overall, the full model was significant as compared to the null model (comprising test subject age, random factors, and random slopes) for the response variable licking (LRT: $\chi^2=7.708$, $df=2$, $P=0.021$) but not for nose within 15 cm ($\chi^2=0.292$, $df=1$, $P=0.589$). More specifically, we found that males licked significantly more often than females and that age tended to have a positive effect on licking (Table 5) which supported the results of the previous model. However, co-residence did not appear to have an effect on the number of licking (Table 5).

Discussion

In the current study, we present the first field bioassay conducted on olfactory group recognition using body odor in semi-free-ranging primates that do not possess distinct scent glands. Overall, our results suggest that rhesus macaques are able to distinguish between familiar in-group and unfamiliar out-group individuals via olfactory cues alone.

Olfactory recognition of group members

Specifically, we found that both males and females place their nose close to the odors of unfamiliar out-group females for longer periods than to the odor of familiar female group members. This result is in line with our prediction and supports previous findings regarding group recognition in mammalian species such as dogs (Dunbar and Carmichael 1981), horses (Péron et al. 2014), or Columbian ground squirrels (Harris and Murie 1982). In primates, for example, common marmosets (*C. jacchus*) also directed significantly more investigatory behavior to the scent from unfamiliar females as compared to

Table 3 Results of the general linear mixed models (GLMMs) with Gaussian error structure for the response variables nose within 15 cm, sniffing, PC1 (including looking and time spent within 2 m), and handling

Response variable	Predictor variable	Estimate	SE	χ^2	*P*
Nose within 15 cm	Intercept	1.229	0.230	[a]	[a]
	Condition (ref=in-group)	0.646	0.195	8.168	*0.004*
	Sex (ref=female)	−0.179	0.299	0.355	0.551
	Age	−0.130	0.160	0.640	0.424
	Group rank difference	−0.276	0.121	3.445	0.063
	Ambient air time	0.141	0.122	1.305	0.253
Sniffing	Intercept	0.436	0.072	[a]	[a]
	Condition (ref=in-group)	0.104	0.095	[a]	[a]
	Sex (ref=female)	0.229	0.151	[a]	[a]
	Age	−0.062	0.044	1.953	0.162
	Group rank difference	0.008	0.041	0.042	0.838
	Ambient air time	0.043	0.040	1.116	0.291
	Condition × sex	−0.275	0.141	3.732	0.053
PC1 (looking and time spent within 2 m)	Intercept	−0.287	0.229	[a]	[a]
	Condition (ref=in-group)	0.238	0.236	[a]	[a]
	Sex (ref=female)	−0.141	0.346	[a]	[a]
	Age	−0.291	0.161	3.140	0.076
	Group rank difference	0.030	0.199	0.021	0.884
	Ambient air time	0.177	0.106	2.293	0.130
	Condition × sex	0.233	0.304	0.561	0.454
Handling	Intercept	0.212	0.073	[a]	[a]
	Condition (ref=in-group)	0.115	0.084	[a]	[a]
	Sex (ref=female)	0.069	0.112	[a]	[a]
	Age	−0.080	0.047	2.893	0.089
	Group rank difference	−0.061	0.038	2.510	0.113
	Ambient air time	−0.001	0.039	0.000	0.985
	Condition × sex	−0.022	0.125	0.030	0.862

Note that for the response variable nose within 15 cm, a reduced model was run without the interaction condition × sex since the effect of the interaction was not significant. Results for the interaction of the full model are indicated in the text. Indicated are the estimates, standard errors (SEs), chi-square values (χ^2). and *P* values. Degrees of freedom (*df*s) were 1 throughout. Significant effect is marked in italics

ref reference level

[a] Not shown because of not having a reasonable interpretation

familiar females (Smith et al. 1997). Likewise, tufted capuchins (*Cebus apella*, Ueno 1994) and two species of lemurs, *Lemur fulvus* and *Lemur macaco* (Fornasieri and Roeder 1992), investigated the scent of non-group individuals

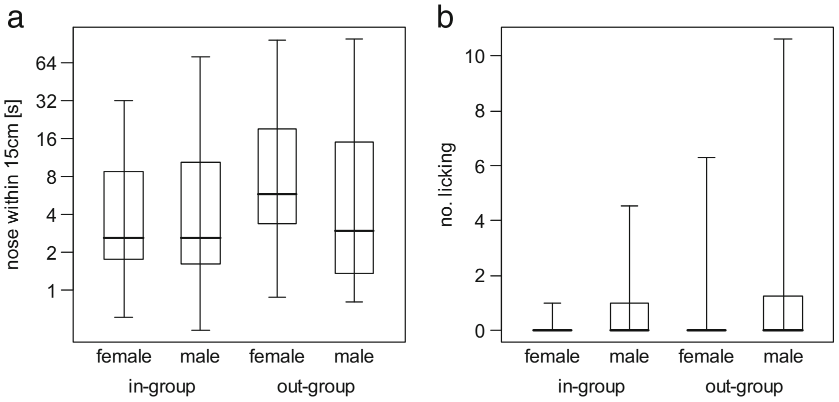

Fig. 2 Durations or counts of response behaviors towards female body odors per sex and test condition. Indicated are the median (*thick horizontal lines*), quartiles (*boxes*), and percentiles (2.5 and 97.5 %; *error bars*) for **a** nose within 15 cm (note that the *y*-axis is on a log scale) and **b** licking

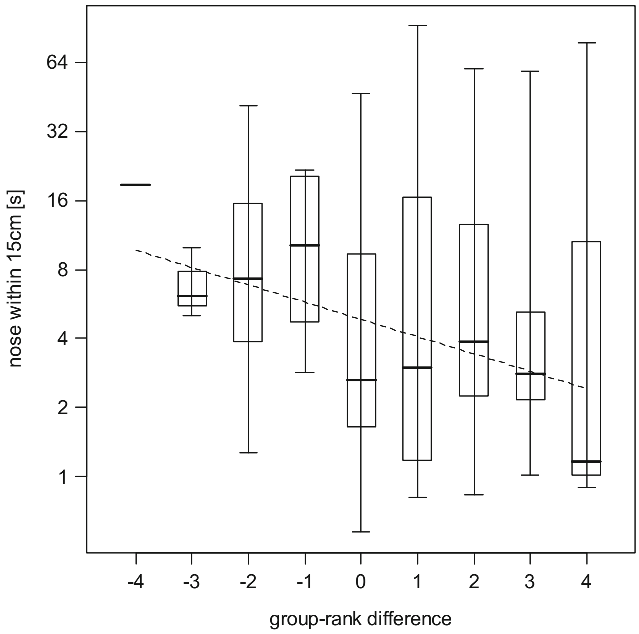

Fig. 3 Box plots showing the influence of the group rank difference between test subject and odor donor on the duration the test subjects placed their nose close to the odor. Indicated are the median (*thick continuous horizontal lines*), quartiles (*boxes*), and percentiles (2.5 and 97.5 %; *error bars*). The *dashed line* represents the results of the fitted model. Group rank difference is calculated as group rank of test subject–group rank of odor donor, i.e., the duration of nose within 15 cm was longer the lower the relative rank of the test subjects' group is compared to the odor donors' group

Table 5 Results of the GLMM with Gaussian (for nose within 15 cm) and Poisson error structure (for licking) examining whether the level of familiarity towards the odor donor, indicated by the common presence in days in the same group (co-residence), influences the response behavior of the test subject

Response variable	Predictor variable	Estimate	SE	χ^2	*P*
Nose within 15 cm	Intercept	1.166	0.335	[a]	[a]
	Co-residence	0.152	0.280	0.292	0.589
Licking	Intercept	−2.444	1.044	[a]	[a]
	Co-residence	−0.269	0.519	0.246	0.620
	Sex (ref=female)	2.049	0.917	5.770	*0.016*
	Age	0.559	0.270	3.014	0.083

Note that all significant variables from the previous models are included. Indicated are the estimates, standard errors (SEs), chi-square values (χ^2), and *P* values. Degrees of freedom (*df*s) were 1 throughout. Significant effect is marked in italics

ref reference level

[a] Not shown because of having no meaningful interpretation

significantly longer than the scent of their own group members. Generally, group members interact more frequently and are in closer spatial proximity to each other than to conspecifics of other groups and therefore have a greater chance to perceive and potentially learn the smell of familiar individuals compared to that of out-group individuals. Since rhesus macaque groups move coherently several times a day (Boelkins and Wilson 1972), the ability to distinguish between familiar group members and unfamiliar non-group members might be important to regulate group movements by orienting towards the odor of familiar individuals as well as for the regulation of social interactions with neighboring groups.

In contrast to our expectation, males and females did not appear to react differently towards female out-group odors, indicating that the recognition of out-group females appears to be equally important for both males and females in the non-

Table 4 Results of the generalized linear mixed models (GLMMs) with Poisson error structure for the response variables licking and self-scratch

Response variable	Predictor variable	Estimate	SE	χ^2	*P*
Licking	Intercept	−3.188	0.705	[a]	[a]
	Condition (ref=in-group)	0.852	0.573	2.177	0.140
	Sex (ref=female)	1.677	0.609	7.565	*0.006*
	Age	0.798	0.297	7.038	*0.008*
	Group rank difference	0.157	0.294	0.294	0.588
	Ambient air time	−0.420	0.355	1.423	0.233
Self-scratch	Intercept	−2.433	0.775	[a]	[a]
	Condition (ref=in-group)	−0.199	0.893	[a]	[a]
	Sex (ref=female)	0.653	0.973	[a]	[a]
	Age	−0.292	0.432	0.506	0.477
	Group rank difference	0.825	0.472	2.895	0.089
	Ambient air time	−0.108	0.321	0.113	0.737
	Condition × sex	−0.985	1.028	0.911	0.340

Note that for the response variable licking, a reduced model was run without the interaction condition*sex since the effect of the interaction was not significant. Results for the interaction of the full model are indicated in the text. Indicated are the estimates, standard errors (SEs), chi-square values (χ^2), and *P* values. Degrees of freedom (*df*s) were 1 throughout. Significant effects are marked in italics

[a] Not shown because of not having a reasonable interpretation

mating season. According to the socioecological model (Wrangham 1980), environmental risks and resources determine the spatial and temporal distribution of females, which then sets male strategies for monopolizing fertile females (Altmann 1990; Nunn 1999). Females are generally more dependent on resources such as food, water, and sleeping sites than males due to their enhanced investment in rearing offspring. When intergroup fights take place in rhesus macaques, it usually involves adult females, standing in the first line when fighting in *line formation* (Koford 1963; Hausfater 1972), a phenomenon that can be found in other macaque species as well (e.g., Japanese macaques, *Macaca fuscata*, RT, personal observation). As a result, females may be selected for recognizing out-group individuals to defend their resources. For males, mate choice might constitute a more likely selective pressure for recognizing out-group females. In several primate species, females choose out-group males as mating partners (e.g., savanna baboons, *Papio cynocephalus anubis*, Bercovitch 1991; vervet monkeys, *Cercopithecus aethiops*, Henzi and Lucas 1980; long-tailed macaques, *Macaca fascicularis*: van Noordwijk 1985; siamangs, *Hylobates syndactylus*, Palombit 1994). Rhesus macaque males have also been reported to exhibit extra-group mating (Brereton 1981; Berard et al. 1993), with 24.7 % of the infants being sired by out-group males (Widdig et al. 2004), and females actively choose out-group males as mates under certain circumstances (Manson 1995). Thus, it might be important for males to recognize out-group females even in the non-mating season to prospect for future mating partners.

However, we might expect a different response pattern during the mating season, with males showing even more interest in the odor of out-group females than females. Macaques are highly seasonal breeders, and males have been observed to frequently sniff and lick at female genitalia at the onset and during the mating season (SH, personal observation). As previously demonstrated, males do not have the physiological preconditions for successful mating all year round as spermatogenesis is strictly restricted to the mating season (Thomsen and Soltis 2004). Since males' interest towards females is mainly driven by sexual motivation, it is likely that males show even higher olfactory response behaviors in the mating season. Future studies should thus compare rhesus macaques' olfactory discrimination abilities between the mating and non-mating season.

Our results further indicate that males licked female odors, in general, more often than females. Whereas sniffing serves to gather olfactory information on volatile compounds of an odorant (processed by the olfactory epithelium), animals mostly perceive non-volatile signals by licking for the assessment by the vomeronasal organ (Keverne 1999; Scordato and Drea 2007; Drea et al. 2013). Since males frequently sniff and lick at female genitalia, especially during the mating season (SH, personal observation), they might gather information about female fertility status. However, recent evidence suggests that rhesus males have limited information regarding the exact timing of female fertility as their mate-guarding efforts are not perfectly correlated with female ovulation (Dubuc et al. 2012). If and to what extent males can assess female fertility status via olfactory cues remains to be tested in future studies.

In addition, we found that age had a positive effect on the number of licking. This result is surprising, given that previous findings indicate that younger individuals generally inspect novel objects more frequently than older ones (e.g., Joubert and Vauclair 1986; Bergman and Kitchen 2009). However, since these studies compared behavioral responses between immature and adult individuals, the relationship appears to be different when considering only adults as in the present study.

While significant results were obtained for the olfactory investigatory behaviors nose in proximity and licking, non-olfactory behavioral responses, such as looking and being in vicinity, handling, or self-scratching, did not seem to be affected by the in-group versus out-group condition, indicating that discrimination is only occurring in behaviors that are directly connected with perceiving the scent stimulus.

Effect of co-residence on the response behaviors in the in-group condition

In the present study, we additionally investigated whether the response behaviors in the in-group condition depend on different levels of familiarity, expressed by the co-residence in the same group of the test subject and the odor donor. Generally, not all individuals might have access to information regarding the smell of all or many of their group members and this is particularly likely for non-natal adult males who recently immigrated. Thus, the level of familiarity between a dyad of individuals within a group might vary with their co-residence in the same group. Our results indicate, however, that co-residence does not affect response behaviors. We suggest that relationships between two individuals may, rather than their mere co-residency history, be an influential factor for response behaviors which gives interesting prospects for future studies.

Effect of group rank difference

Our results further suggest that the strength of the olfactory response behavior tends to depend on the rank difference between the group of the test subject and that of the odor donor. The lower the rank of the group of the test subject compared to the group rank of the odor donor, the greater is the response when investigating the odor by nose. Likewise, the higher the rank of the group of the test subject compared to the group rank of the odor donor, the shorter is the investigation time by nose. This finding suggests that individuals appear to know the status of their own group as well as the one of the foreign group, which they seem to assess via olfactory signals. This means, furthermore, that they can possibly put their status into relation to each other and that they regulate their behavior accordingly. There is great evidence that primates have a detailed understanding of their social environment, not only of other group members but also of their complex social relationships (reviewed in Bergman and Sheehan 2013). For example, it has been demonstrated that male bonnet macaques (*Macaca radiata*) use information about the relative ranks of other males in their group to recruit allies (Silk 1999). Chacma baboons recognize relative ranks of rivals (Kitchen et al. 2005) and respond differently to males that are climbing or falling the hierarchy (Bergman et al. 2006). However, the awareness of the status of one's own social group as an entity in relation to the status of another group has, to our knowledge, not been demonstrated yet. As this tendency was only present in one response variable, further investigations are needed to shed light into the understanding of group identity within non-human primates.

Effect of odor sample reuse

In the present study, we tested for the effect of odor sample reuse on odor intensity as well as on the duration or number of the test subjects' response behaviors. Although the intensity of odor samples, assessed by human raters, seemed to decrease with proceeding use over the course of a given test day as well as over the whole study period, reuse did not have an effect on rhesus macaques' response behaviors. Repeated thawing did not affect odor sample quality in humans (Lenochova et al. 2008; Roberts et al. 2008), which can be supported by our results in rhesus macaques. Thus, our findings are important for setting up experimental standards for future behavioral studies in mammalian olfactory communication, especially when using odor samples in the field and when a limited availability of odor samples requires their reuse. We further conclude that intensity scores can be considered as a reliable estimate of odor intensity and can be a valuable means for future studies.

Importance of olfactory cues at night and during periods of reduced visibility

Whereas visual signals might be of more importance for recognizing out-group conspecifics during the day, olfaction might be the crucial sense in early morning hours and twilight as well as during the night. Boelkins and Wilson (1972) found that most of the seriously aggressive intergroup encounters on Cayo Santiago took place at dusk when catarrhine primates' visibility is limited. Furthermore, although rhesus macaques are diurnal animals and their activity is highly photoperiod dependent (Hauty and Yellin 1970), they show bursts of activity throughout the night including moving, vocalizing, feeding, and playing (Vessey 1973). Peripheral rhesus macaque males (sneaker males) or high-ranking males of other groups were shown to initiate fights with out-group males during the night (Vessey 1973), and the escape of individuals from attacking groups or loner males at night was also observed in different groups of western gorillas (cf. Krief et al. 2014). During mating season, fights at night are even more frequent and, also, copulations occur frequently at night (Vessey 1973). Males stay in consortship with the females during the night to defend them against sneaker males. In Barbary macaques (*Macaca sylvanus*), sneaker males indeed copulated successfully with females at night (Berghänel 2009). The ability to recognize non-group individuals via olfactory cues might thus be of great advantage and may increase reproductive success and survival. Furthermore, the distinction between familiar and unfamiliar individuals via olfactory cues might be crucial for the regulation of group movements at night.

Olfaction may also constitute an important communication mode in wild-living catarrhine primate species that reside in dense forest habitats, where visibility is limited during daytime as well. Male chimpanzees (*P. troglodytes troglodytes*), a species without distinct mating season, for example, were reported to sniff the ground and vegetation while patrolling along the borders of their territory (Mitani and Watts 2005; Herbinger et al. 2009). Chimpanzee males are known to be highly territorial all year round and to kill stranger males (Watts and Mitani 2001; Boesch et al. 2008). Since odorants can persist for longer periods of time, olfactory cues may convey information about individuals even without them being present. Although it is still discussed why male chimpanzees sniff the borders of their territory, we could assume that, based on our findings in rhesus macaques, they may heavily rely on the olfactory sense in search of long-lasting body odor marks of out-group males.

Possible recognition mechanisms

The recognition of group members versus out-group individuals via olfactory cues could be explained by three possible mechanisms. First, a mutual group odor exists which differs from that of all other groups. Colony scents are known in social insects (Breed 1983; Bonavita-Cougourdan et al. 1987; Lenoir et al. 1999; Bruschini et al. 2011) as well as nest odors in birds (Bonadonna et al. 2003), but group-specific social odors have also been demonstrated in mammals such as the big brown bat, *Eptesicus fuscus* (Bloss et al. 2002) or the European badger, *Meles meles* (Buesching et al. 2002). The fermentation hypothesis suggests that group-specific scents were derived from different compositions of odor-producing bacteria which are shared between group members through cross infection, resulting from occupying the same space, interacting frequently with each other, and/or consistently scent marking the same sites (Archie and Theis 2011).

Recent studies on spotted hyenas, *Crocuta crocuta* (Theis et al. 2012), and meerkats, *Suricata suricatta* (Leclaire et al. 2014), showed that microbial communities in scent gland secretions are more similar within groups than between groups. In primates, scent marking and urine washing are common among strepsirrhines as well as New World monkeys and are regarded as a means of group cohesion and recognition (Ziegler 2013). Although rhesus macaques do not seem to possess scent glands and do not exhibit scent marking or urine washing behavior (Geissmann 1987), it might still be possible that individuals recognize their group members via a social group odor which is in line with our finding that group rank difference tends to have an effect on olfactory investigatory behavior. Alternatively, it might be likely that group recognition is based either, secondly, on the individual recognition of one's group members or, thirdly, on familiarity. Hence, subjects might respond more strongly to out-group odors either because they are simply unfamiliar and therefore more interesting or because they recognize them as members of another group. In each of the two latter scenarios, individuals would be able to memorize the odor identities of their group members which, in our study population, can comprise up to 330 individuals. The present study does not allow us to determine which of the three mechanisms is responsible, but it does suggest that the rhesus macaques of Cayo Santiago are able to discriminate odor of current group members from out-group individuals. If or to what extent microbiota play a role in determining individual or group-specific odors in primates remains an interesting area for further research.

Together, although our results suggest that rhesus macaques are able to distinguish between in-group and out-group individuals based on olfactory cues alone, the recognition of conspecifics might be a more multimodal process including visual cues or a combination of olfactory and auditory signals as recently demonstrated in ring-tailed lemurs (Kulahci et al. 2014). Further research is required to fully understand the underlying mechanisms of recognition processes, but the findings of our study indicate that olfactory communication might play a much greater role in catarrhine primates' societies as previously assumed.

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Ethical standards This study was conducted in accordance with the guidelines of the Association for the Study of Animal Behaviour/Animal Behavior Society for the use of animals in research, the legal requirements of the country in which the work was carried out, and all institutional guidelines. All research procedures were approved by the CPRC and the Institutional Animal Care and Use Committee (IACUC) of the University of Puerto Rico (protocol number 4060105).

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