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Social shaping of voices does not impair phenotype matching of kinship in mandrills

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Kin selection theory provides a strong theoretical framework to explain the evolution of altruism and cooperative behaviour among genetically related individuals. However, the proximate mechanisms underlying kin discrimination, a necessary process to express kin-related behaviour, remain poorly known. In particular, no study has yet unambiguously disentangled mechanisms based on learned familiarity from true phenotype matching in kin discrimination based on vocal signals. Here we show that in addition to genetic background, social accommodation also shapes individual voices in an Old World monkey (Mandrillus sphinx), even though primate vocalizations were thought to be innate and little flexible. Nonetheless, social shaping of voice parameters does not impair kin discrimination through phenotype-matching of unknown relatives, revealing unexpected discriminatory versatility despite signal complexity. Accurate signal production and perception, therefore, provide a basis for kin identification and kin-biased behaviour in an Old World primate.

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Despite ongoing controversies surrounding the importance of kin selection (for example, refs 1,2), empirical studies have repeatedly demonstrated its major role in determining social relationships in various animal societies3–4. Whereas kin bias in social behaviour is widespread, the proximate mechanisms underlying the ability to recognize kin remain poorly studied, with the exception of laboratory rodents5–8. Groups of non-human primates are characterized by the co-residence of individuals belonging to various kin classes and showing variable social bonds7. Most groups are also characterized by stable cores of maternally related females (matrilines), enduring mother–offspring bonds and male-biased dispersal4,8. Learning direct of maternally related females (matrilines), enduring mother–

Results and Discussion

Familiarity and genetic ties impact mandrill vocalizations. We show that the acoustic structure of contact calls recorded from 36 male and female mandrills (Supplementary Table 1) with different levels of relatedness and familiarity (Supplementary Tables 2 and 3) is more similar among relatives than among unrelated individuals, when controlling for other confounding effects (see Methods), including familiarity (calculated as the number of years spent in the same social group). Indeed, of the seven acoustic variables examined to characterize the vocal signature of individuals, genetic relatedness alone or genetic relatedness in interaction with familiarity influence four out of five variables belonging to the spectral domain and one out of two variables belonging to the temporal domain (General Linear Mixed Model—LMM; Table 1 and Fig. 1; see Methods). Moreover, the resulting acoustic distance across dyads in the space defined by the first two principal component analysis (PCA) components calculated from the seven orthogonally transformed acoustic variables (Euclidean acoustic distances) is also significantly influenced by relatedness in combination with familiarity (LMM, N = 630 dyads, F_{1,628} = 7.87, P = 0.0052; Table 1). Acoustic distance decreases with familiarity but this decrease is more pronounced when relatedness is low (Supplementary Fig. 1). In particular, among unfamiliar dyads—the ones that have never experienced any form of social contact—the highly related dyads are the ones that are acoustically the most similar (Fig. 2a). Our results further indicate that familiarity and relatedness tend to have an impact on acoustic parameters in different ways (Table 1). Although it is unlikely that any of the acoustic variables is entirely innate or learned, some acoustic variables might be more influenced by relatedness (‘innate’ features) and thus should be less flexible than those more influenced by familiarity (‘learned’ features). For instance, a variable representing the fluctuation of the mean frequency (that is, SD frequency) should

| Table 1 | Predictors of seven acoustic variables. |
|-----------|----------------------------------------|
| **LRT1 (D, P)** | **LRT2 (D, P)** | **Response variables** | **Explanatory variables (f, P)** |
| Population | Sex | Age | Rank | Familiarity | Relatedness | Familiarity × Relatedness |
| 42.5, <0.001 | 22.6, <0.001 | Acoustic distance | 0.01, 0.94 | 1.21, 0.30 | 0.26, 0.61 | 0.07, 0.79 | 11.58, 0.0007 | 10.11, 0.0016 | 7.87, 0.0052 |
| 34.1, <0.01 | 22.3, <0.001 | MEAN | 0.37, 0.54 | 0.12, 0.89 | 0.01, 0.93 | 0.05, 0.82 | 2.53, 0.11 | 6.93, 0.0087 | 4.22, 0.0405 |
| 45.1, <0.01 | 17.5, <0.01 | SD | 1.98, 0.16 | 5.00, 0.077 | 0.45, 0.50 | 0.75, 0.39 | 12.82, 0.0004 | 4.58, 0.0328 | 3.66, 0.0562 |
| 31.1, 0.86 | 17.7, 0.89 | Q25 | 2.44, 0.12 | 2.77, 0.71 | 0.74, 0.09, 0.76 | 0.36, 0.55 | 0.73, 0.39 | 4.08, 0.029 | 10.72, 0.0011 | 4.05, 0.0446 |
| 52.4, <0.001 | 24.0, <0.001 | Q75 | 0.04, 0.84 | 0.82, 0.44 | 0.05, 0.83 | 0.01, 0.93 | 4.80, 0.029 | 14.63, 0.0001 | 8.12, 0.0046 | 5.66, 0.0177 |
| 35.9, <0.01 | 16.3, <0.01 | IQR | 0.94, 0.33 | 1.92, 0.15 | 0.94, 0.33 | 0.17, 0.68 | 7.09, 0.008 | 0.12, 0.73 | 2.92, 0.0881 |
| 24.5, 0.11 | 15.7, <0.01 | DURATION | 0.18, 0.68 | 0.86, 0.42 | 0.32, 0.57 | 0.57, 0.45 | 7.89, 0.0049 | 9.16, 0.0026 |
| 28.6, 0.04 | 11.9, 0.04 | ICI | 0.21, 0.65 | 1.93, 0.15 | 2.99, 0.08 | 0.14, 0.71 | 6.19, 0.013 | 7.98, 0.0049 |

General Linear Mixed Models (Proc GLM, SAS, V9.4) based on the acoustic distance between pairs of individuals (Euclidean distance calculated from the individual coordinates obtained from the two first components of the PCA) and on the absolute differences between pairs of individuals for each of the seven studied acoustic variables and their relationships with different explanatory variables (f values and P values are displayed). Significant (P ≤ 0.05) or marginally significant (P < 0.10) explanatory variables are shown in bold or in italics (respectively) after Holm Bonferroni corrections for multiple testing (P values are not corrected). Log-likelihood Ratio Tests (LRT) are displayed to compare each full model (with all predictors including the interaction effect of relatedness and familiarity—the LRT1 with corresponding null model and each full model with the interaction effect with the corresponding model without the interaction effect (LRT2; the test statistic D and P values are both displayed). Full models for Q25 and DURATION performed as good as their associated null models; full model with the interaction effect for Q25 performed as good as full model without the interaction effect.
Indeed, the degree of familiarity influences individual acoustic signals convey reliable information on genetic relatedness and, thereby, modifies individual voices. For example, maternal half-siblings tend to be acoustically more similar than paternal half-siblings (Table 2b; Fig. 3). Interestingly, maternal half-siblings exhibit more similarity in their acoustic features than non-kin dyads (LMM, N = 69 dyads, F₁,68 = 11.33, P = 0.002; LRT: D = 18.4, P < 0.01; Fig. 2b).

Finally, the study of the effect of kin classes, considering maternal half-siblings, paternal half-siblings and non-kin dyads alone (N = 100 dyads), revealed a significant effect of kinship in combination with the degree of familiarity of the dyad: maternal and paternal half-siblings are acoustically more similar than non-kin dyads, especially when they are unfamiliar or little familiar with each other (LMM, N = 100 dyads, F₃,97 = 4.86, P = 0.013; Table 2a; Fig. 3). Interestingly, maternal half-siblings tend to be acoustically more similar than paternal half-siblings (Table 2b; Fig. 3), despite similar relatedness coefficients (r ~ 0.25).

Taken altogether, these results indicate that mandrill vocal signals convey reliable information on genetic relatedness and that social accommodation further modifies individual voices. Indeed, the degree of familiarity influences individual acoustic features, and unrelated but familiar individuals exhibit voice similarities. In addition, maternal half-siblings appear to be the most acoustically similar kin (albeit only showing a non-significant trend in this direction in comparison with paternal half-siblings). These maternal kin live in a more close-knit social environment than do paternal half-siblings. Social environment (familiarity) and probably social ties (maternal kinship) may therefore modulate voice features, as does genetic information. Whereas vocal plasticity at the individual level is well documented in songbirds, parrots, dolphins and seals, studies showing socially guided flexibility in primate calls are still sparse (for example, refs 25–27). Conversely, several studies have shown the vocal repertoire of primates to be fixed and genetically determined. For example, social isolation or early deafness does not prevent squirrel monkeys from spontaneously producing the full vocal repertoire of their species. Cross-fostered macaques raised with individuals from a different species still continue to produce their own species-specific calls. Genetic factors therefore seem to determine the general species-specific vocal repertoire of a primate species; however, social factors can modify some calls, which may then function as a 'social badge' in the same way as described for humans.

**True phenotype matching in mandrills is based on vocal cues.** Using playback experiments, we tested the phenotype-matching hypothesis by studying 101 sender–receiver dyads with different levels of relatedness and familiarity (Supplementary Table 3). We found that receivers respond more intensely (more body and head movements) to the calls of related senders (Generalized Linear Mixed Model—GLMM; controlling for other factors: F₁,99 = 7.12, P = 0.010; Table 3 and see Methods). In contrast, the degree of

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**Figure 1 | Acoustic differences across dyads as a function of their genetic relatedness for seven variables.** The seven variables belong to (a) the spectral domain (mean frequency ‘MEAN’ in red, s.d. of the mean frequency ‘SD’ in purple, first quartile ‘Q25’ in orange, third quartile ‘Q75’ in blue, interquartile range ‘IQR’ in green) and (b) the temporal domain (call ‘DURATION’ in pink, intercall interval ‘ICI’ in light green). For the sake of clarity, we represent average acoustic differences (± s.e.m.) as a function of three levels of relatedness. The three spectrograms (c) on the right of the figure illustrate the acoustic similarity between calls according to relatedness: mandrills 1 and 2 are unrelated (r = 0); mandrills 1 and 3 are related (r = 0.53).
Evidence for the importance of acoustic kin discrimination has also recently been found in two other primate species. Captive female-grey mouse lemurs (*Microcebus murinus*) responded differently to calls from their fathers compared with unrelated males, and female rhesus macaques (*Macaca mulatta*) responded more often to calls from unfamiliar paternal half-sisters than to those from unrelated females. However, female lemurs and their fathers were kept together as adults for variable periods of time so that caller identity could have been linked to other cues of relatedness. Moreover, the unfamiliar pairs in the macaque study, although from different social groups, lived on the same small island where intergroup encounters are frequent. Direct familiarity among subjects can therefore also not be completely excluded. Our study, therefore, unravels a proximate mechanism that plays a significant role in kin-discrimination processes, demonstrating unequivocal support for the phenotype-matching hypothesis through vocal signals.

Table 2 | Kinship and acoustic distance.

**(a)** Explanatory variables

| Population | Sex | Age | Rank | Kin class | Familiarity | Kin class × familiarity |
|------------|-----|-----|------|----------|------------|------------------------|
| F          | P   | F   | P    | F        | P          | F                      |
| 1.19       | 0.28| 0.17| 0.85| 0.0005   | 0.62       | 0.28                   |

**(b)**

| Explanatory variables | Estimate | t | P value |
|-----------------------|----------|---|---------|
| MS-NK                 | 0.66     | 4.15 | 0.0002  |
| PS-NK                 | 0.37     | 2.90 | 0.0062  |
| MS-PS                 | 0.29     | 1.87 | 0.069   |

MS, maternal half-siblings; NK, non-kin; PS, paternal half-siblings.

The full model with the interaction effect between familiarity and relatedness (a) is statistically better than both the null model (LRT: *D* = 39.8, *P* < 0.001) and the model without the interaction effect (*D* = 10.4, *P* > 0.01). Differences in least-square means (b) are shown.

In summary, our study reveals that primate vocalizations can be shaped by both genetic factors and social experience. Mandrills’ contact calls contain information about genetic relatedness and the degree of familiarity between individuals. Mandrills are also able to rely on these complex vocal signals alone to discriminate unknown kin from non-kin. Accurate signal production and perception therefore provide a basis for kin identification and kin-biased behaviour. Because mechanisms of phenotype matching rely on communication systems that include the emission of signals, their transmission throughout the environment and their reception and processing by receivers, imperfect coding or decoding may occur along this chain. Other communication channels might, therefore, be involved simultaneously to reinforce the signal. Mandrills live in large groups comprising several hundred individuals, and both visual and olfactory signals may signal relatedness at short distances. In contrast, in closed forest habitats, vocal signals may enable individuals to adjust their behavioural responses to more distant senders. The present study on acoustic kin discrimination in
Table 3 | Predictors of playback responses.

| Explanatory variables | F  | P  |
|-----------------------|----|----|
| Receivers’ characteristics |    |    |
| Sex                   | 0.04 | 0.85 |
| Age                   | 0.10 | 0.76 |
| Rank                  | 0.36 | 0.70 |
| Sender’s characteristics |    |    |
| Age                   | 0.96 | 0.33 |
| Rank                  | 0.90 | 0.41 |
| Population identity   | 0.85 | 0.36 |
| No. of emission of call sequences | 3.19 | 0.080 |
| No. of other movements | 8.01 | 0.007 |

Relatedness and familiarity

- **Relatedness**: 7.12 | 0.010
- **Familiarity**: 0.83 | 0.37

Generalized Linear Mixed Model (Proc GLIMMIX SAS V9.4) based on the number of movements displayed towards the speaker. Significant (P < 0.05) predictors are shown in bold. The full model is statistically better than the null model (LRT: D = 44.3, P = 0.000), Note that the model including the interaction between relatedness and familiarity does not perform better than the full model without the interaction (D = 0.02, P = 0.88).

Figure 4 | Playback responses and genetic relatedness. The playback responses (average number of movements displayed towards the speaker ± s.e.m.) as a function of sender-receiver’s genetic relatedness, across all dyads (light grey) and across unfamiliar dyads only (dark grey) are shown. For the sake of clarity, three classes of genetic relatedness are represented. Sample sizes for each relatedness level are given (numbers within bars).

Acoustic analyses. In April 2013, we recorded contact calls (‘kakak’) of 36 males and females (Supplementary Tables 1 and 2). These calls are naturally produced by females of any age and non-adult males when the group starts to move and more generally when individuals need to know where conspecifics are (see also ref. 37). These calls are composed of typical sequences of several consecutive calls (on average eight calls per sequence, range 2–21, N = 84 sequences; Fig. 1 and Supplementary Audio Files 1–3). Mandrill contact calls have a wide frequency spectrum and a harmonic structure that is more visible for males than for females (Fig. 1). They are short in duration (mean ± s.d.: 33 ± 9 ms) and can be modulated in frequency and amplitude (Supplementary Table 1). Contact calls were recorded with a Sennheiser MKH70 ultra directional microphone connected to an H4n ZOOM digital recorder (resolution: 16 bits; sampling rate: 44.1 kHz; Waveform Audio File format).

Recordings were performed during direct observations of mandrills foraging in clear forest understory for the wild population and around feeding time from an observation platform for the semi-free population. Recordings were all performed between 5 and 10 m from the sender, with no obstacle between the sender and the microphone. The identity of each sender was immediately double-checked with at least one additional observer.

We extracted temporal and spectral parameters from 526 calls of 84 sequences of contact calls displayed by 36 individuals (mean ± s.d.: 14.6 ± 10.3 calls per an Old World primate therefore reveals an unexpected discriminatory versatility despite previously unknown signal complexity.

Methods

Population information. We studied three mandrill populations living in southern Gabon. A semi-free ranging population (hereafter termed ‘semi-free population’) composed of ~200 individuals lives in two contiguous forested enclosures (9.5 ha) at the Centre International de Recherches Médicales de Franceville (CIRMF). CIRMF also houses a captive population (hereafter termed ‘caged population’) composed of 120 individuals living in a private park in southern Gabon (Parc de la Lékédi, Bakoumba). About 20% of the individuals from this population originated from the semi-free ranging population from CIRMF, released in 2002 and 2006. From 2002 on, wild adult and sub-adult males immigrated into this group and sired offspring with the released females and their descendants. Again, the two CIRMF populations and the wild population contain individuals that are genetically related to various degrees but that never met. For this study, we recorded calls from a total of 39 individuals belonging to the semi-free ranging (N = 34) and the wild (N = 5) populations (a subset of 36 individuals were used for the acoustic analyses including the five wild animals; see below), and we performed playback tests on 13 captive receivers (Supplementary Table 2).

Individuals in all three populations are habituated to humans and are individually recognized as a result of daily population monitoring. Behavioural follows-ups allowed us to determine the exact age of all study individuals and to assign a dominance rank, unambiguously attributed following methods based on approach-avoidance behaviour. In all subsequent analyses, we considered three classes of dominance rank (high-, mid- and low-ranking animals).

All individuals of the three mandrill populations are regularly captured using blowpipe intramuscular injections of anaesthetics (for example, refs 16,36), and blood samples are collected on every occasion. DNA extractions from white cells were performed using QIAamp DNA Blood Mini Kits (Hilden, Germany) and microsatellite genotyping was carried out using 12 primer pairs (as per ref. 16). Pedigree analyses were performed using Cervus 3.0 software described previously. We were able to reconstruct the full pedigree of all study individuals, going back as far as the generation of the founder animals that were all unrelated (four to five maternal generations in total). We also reconstructed the full pedigree of each of the five sampled wild animals, all of which originated from the semi-free ranging population. For each dyad (sender–receiver), we performed a acoustic analysis and sender–receiver (for the playback analysis), we were therefore able to assign an exact coefficient of genetic relatedness. For example, mother–offspring dyads were related at 0.5. However, most studied dyads were related both through the paternal and the maternal lines (of ‘mixed origin’ as in Supplementary Table 3) because of limited genetic drift. For the acoustic analyses alone, sample sizes allowed distinguishing dyads of true non-kin from paternal and maternal half-siblings. In these analyses, paternal half-siblings did not come from the same matriline and paternal half-siblings did not share a comon father. By contrast, in the playback analyses, limited sample sizes did not allow examining differences among kin classes.

In all our analyses, we were also able to control for the degree of familiarity between individuals. Two individuals were considered as familiar when they experienced any form of social contact during a stage of their life. Familiar individuals spent between 6 months to almost 23 years together (there were no familiar dyads that lived for less than 6 months together in the studied population; mean ± s.d. across all studied dyads: 4.5 ± 4.3 years). In the following analyses, we considered the number of years living in the same social environment rounded to the higher nearest integer as a conservative estimate of familiarity. However, because some of the dyads were familiar to each other several years ago (then subsequently separated), while others were familiar for more than 25 years, we are still familiar, we re-ran all analyses using ancient versus recent familiarity as an explanatory variable. The age of familiarity had an impact on neither the studied acoustic parameters nor the playback responses (Supplementary Note 1).

This study complies with ethical protocols approved by the CENAREST institutional authorization number: AR0003/12/MENSRSC/CG/ CST/CSAR). The research adhered to the legal requirements of Gabon for the ethical treatment of non-human primates.
individual, range: 3–41; 2.4

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absolute differences between all dyads of individuals involving 36 senders (N

call. Three spectral variables described the distribution of energy over the duration

interval; ICI) between the offset of the previous call and the onset of the considered

total duration of calls (hereafter DURATION) and the silence duration (intercall

three classes of kin using differences in least-square means (lsmeans procedure,

half-siblings and maternal half-siblings, as described above. We compared these

strictly unrelated dyads. In a final analysis, we further explored the effect of kinship

distance, restricting our data first to the strictly unfamiliar dyads and then to the

male-male), the difference in age (absolute age difference between members of a

sex composition of the dyad (discrete variable coded female-female, male-female or

Q25, Q75, IQR and DURATION were square root-transformed; ICI was ln-

SAS v9.4) with a Gaussian error structure. Normality of the residuals was attained

features, we first performed General Linear Mixed Models (LMM, Proc GLIMMIX,

the call coordinates. Last, we calculated the Euclidean acoustic distance between all

dyads of individuals based on the individual coordinates.

To sum up, for each dyad, we obtained eight values: one average absolute
difference for each of the seven acoustic variables and one Euclidean acoustic
distance (to study the effects of genetic relatedness and kinship ranging from 0 to 1 among

the study subjects) and familiarity (ranging from 0 to 23 years) on these acoustic

features, we first performed General Linear Mixed Models (LMM, Proc GLIMMIX,

SAS v9.4) with a Gaussian error structure. Normality of the residuals was attained

after applying the following transformations: Euclidean acoustic distance, MEAN,

Q25, Q75, IQR and DURATION were square root-transformed; ICI was In-

transformed; SD was kept untransformed. We further considered the following

predictors as possible confounding covariates: whether the two individuals of the
dyads belonged to the same population or not (discrete variable coded 0 or 1),

the sex composition of the dyad (discrete variable coded female-female, male-female or

male-male), the difference in age (absolute age difference between members of a

dyad) and the absolute difference in dominance rank (continuous variable ranging

from 0 to 2, see above). We also considered the identity of the two senders as two

random effects. Second, we performed two more LMM based on the acoustic
distance, restricting our data first to the strictly unfamiliar dyads and then to the strictly

related dyads (hereafter relatedness). As a final analysis, we included the distance

(continuous variable ranging from 0 to 2, see above). We also considered the identity of the two senders as two

random effects. In a second analysis, we considered the number of

playbacks, number of days, and the order of playback sessions were randomized from

none (only ‘mock sessions’ occurred) to three sessions per day (along with one ‘mock session’). If a

same sequence of calls had to be broadcast more than once, the two sessions were

performed at least 2 days apart. Most of the sequences were used once (60.6% of the

sequences; Supplementary Table 4) according to their relatedness and familiarity

sequences; Supplementary Table 4) according to their relatedness and familiarity

Playback experiments. We selected contact calls of 19 adult females (N = 23

sequences; Supplementary Table 4) according to their relatedness and familiarity

with the ‘receivers’ (Supplementary Tables 2 and 3). The call sequences lasted on

average 984 ± 184 ms and included 96 ± 3.6 calls, each call was spaced on average

by 71.9 ± 41.1 ms of silence. The MEAN frequency of the calls was 1,774 ± 284 Hz.
The sequences were played twice with an interval of 8 s. This coding strategy based

on the redundancy of signals aims to increase the receiver’s attention (see for

review ref. 42). The sequences were prepaped using the GoldWave sound editor v.5.68

to minimize the number of playback sessions already broadcast during the

30-day experimental period (continuous variable ranging from one to five times, see above). This variable was highly correlated with the cumulative number of times each receiver was previously

exposed to playbacks (namely the number of playback sessions already broadcast),

therefore mimicking habituation effects. This cumulative number of times animals

were exposed to playbacks showed the same effect as the number of emissions of

the same sequence of calls and the relatedness of senders (Supplementary Note 2).

We chose to keep the number of emissions of a same sequence of calls in our analysis as a fixed effect. We also considered the number of

body and head movements displayed towards any direction other than the

loudspeaker to correct for the possible hyperactivity of some receivers. Finally,

we considered the identity (N = 13), the relatedness (N = 36) and identity of the

senders (N = 19) and identity of the playback sessions (N = 36) as three

random effects. Over 19 sessions, only four individuals had two different sequences of call

broadcast, precluding the use of an additional random effect of call sequence

identifying the individual to control for differences in the acoustic characteristics

of the playback using the call sequence identity as a random effect rather than the

sender identity. Second, we restricted our data set to a single call per individual

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familiar dyads that never met once in their life. We instead re-ran our model considering only the non-
maternal) ancestries. We further verified the stability of the models by randomly excluding some data
points. Finally, for this playback analysis, we did not replace genetic relatedness by
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Author contributions
L.F. and M.J.E.C. collected data used in this article, performed most of the data analyses and contributed to the writing of the paper. G.C.V. collected data and performed earlier data analyses. A.H., I.L. and E.W. contributed to the writing of the paper. All authors contributed to the conceptual framework of the paper.

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