



Differential patterns of vocal similarity in tolerant and intolerant macaques

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Abstract

The investigation of vocal similarity between individuals has provided evidence of the flexibility of communication signals. This study evaluates the impact of group membership, affiliative bonds, kinship and dominance on acoustic similarity in two primate species with different social styles, intolerant rhesus macaques and tolerant Tonkean macaques. We focused on the fundamental frequencies of the contact calls emitted by adult females. Close kinship promoted vocal similarity between individuals in both species, and also group membership in Tonkean macaques, indicating the involvement of experiential and/or genetic factors. In rhesus macaques more similarities were observed between partners with strong or weak dominance asymmetry than between those with medium asymmetry, which again points to the role of experience. No evidence was found that dominance influences vocal similarity in Tonkean macaques. Our results provide additional evidence to the flexibility of vocal signals produced by macaques, and reveal that it is influenced by social style.

Keywords

learning, vocal communication, dominance, social style, primate.

1. Introduction

For some time now, the literature on animal vocal communication has tended to split animals into two categories, namely vocal ‘learners’ and ‘non-learners’. While the former learn species-specific acoustic structures from conspecific models and have an extensible repertoire (e.g., songbirds, cetaceans, humans) (Snowdon & Hausberger, 1997; Wilbrecht & Nottebohm, 2003; Janik, 2014), the vocal performances of the latter were considered to be driven by a strong genetic determinism that restricts their repertoire to a limited number of call types, as reported in non-human primates (Newman & Symmes, 1982; Hammerschmidt & Fischer, 2008). However, there is now evidence that social influences induce multiple adjustments in the structure of these call types, and that their usage can also be socially learned, particularly in non-human primates (Snowdon, 2017; Cheney & Seyfarth, 2018). A number of studies have shown significant levels of vocal flexibility in monkeys and apes, meaning that the acoustic structures and usages of calls can be modified to some extent through learning (Lemasson et al., 2013; Gruber & Grandjean, 2017; Lameira, 2017).

1.1. Vocal similarity and convergence

The study of vocal similarity and convergence has provided compelling evidence of feedback from the social environment acting upon communication signals. Vocal convergence is a process in which the acoustic properties of the calls emitted by different individuals come to match over time (Snowdon & Hausberger, 1997). It increases acoustic similarity within communities and promotes divergence between communities. This has been reported in songbirds, cetaceans, elephants, bats and primates (Tyack, 2008), but also more recently in gazelles (*Gazella subgutturosa*), goats (*Capra hircus*) and mice (*Mus musculus*), i.e., species that are not considered to possess particular learning abilities (Arriaga et al., 2012; Briefer & McElligott, 2012; Volodin et al., 2014).

Convergence may arise at the interaction level during vocal exchanges between conspecifics. In vocal exchanges, callers modify the acoustic structure of some of their calls to match those of others. This is reported among

female Japanese macaques (*Macaca fuscata*) (Sugiura, 1998), and between mothers and their offspring in gibbons (*Hylobates agilis*) (Koda et al., 2013). In chimpanzees (*Pan troglodytes*), males forming alliances match frequency modulation patterns when chorusing together (Mitani & Gros-Louis, 1998). Moreover, individuals can converge or diverge vocally depending on the context. In a study of female Diana monkeys (*Cercopithecus diana*), the acoustic structure of contact calls diverged between group mates when travelling in a habitat with poor visibility, and calls converged during vocal exchanges (Candiotti et al., 2012). It is worth mentioning that phonetic convergence — or divergence — is also used to signal attitudes between human interlocutors during conversations. This phenomenon is known as vocal accommodation and regulates social inclusiveness (Giles et al., 1991).

Vocal convergence can also arise over the long term from the social relationships between two individuals. In pygmy marmosets, pairing with a new mate led to modifications in trill structure within six weeks, resulting in more homogeneous calls between mates (*Cebuella pygmaea*) (Snowdon & Elowson, 1999). In Campbell's monkeys (*Cercopithecus campbelli*) and bonobos (*Pan paniscus*), two rather tolerant species (Lemasson et al., 2006; Gruber & Clay, 2016), greater similarities were observed between the contact calls of partners that had stronger affiliative bonds (Lemasson et al., 2011) and were same-age peers (Levréro et al., 2019), respectively, and convergence patterns reflected the changes that occurred in social relationships over the years (Lemasson & Hausberger, 2004). In Japanese macaques, a dominance-oriented species, vocal similarity in contact calls was influenced by dominance relationships rather than by affiliative bonds: the higher the rank difference within dyads, the higher the acoustic similarity. This led authors to propose that vocal convergence is a strategy through which subordinates copy the vocalizations of higher-ranking individuals (Lemasson et al., 2016). It is also reported that vocal convergence occurs more frequently between partners of different social status in humans, with the less powerful individual being more likely to modify his/her vocal expression and converge on the other (Gregory & Webster, 1996; Anderson et al., 2003; Pardo et al., 2012).

Vocal similarity has been reported at the group level for contact calls in Japanese macaques and pant hoots in chimpanzees (Crockford et al., 2004; Tanaka et al., 2006). In the latter species, the males of neighbouring communities develop group-specific pant hoots: neighbouring communities

diverged more from each other than from another, geographically distant community (Crockford et al., 2004). The merging of two groups of chimpanzees in captivity induced convergence in the acoustic structure of food grunts, with the newly introduced individuals adopting the structure of the host group (Watson et al., 2015). Interpopulation variations in vocal patterns have also been described in several primate species (Japanese macaques: Green, 1975; Barbary macaques (*Macaca sylvanus*): Fischer et al., 1998; saddle-back tamarins (*Saguinus fuscicollis*): Hodun et al., 1981; red-bellied tamarins (*Saguinus labiatus*): Maeda & Masataka, 1987; chimpanzees: Mitani et al., 1992; pygmy marmosets: de la Torre & Snowdon, 2009). According to the ‘password’ or ‘badge’ hypothesis, shared calls can indicate membership of a given community (Feekes, 1982; Snowdon & Hausberger, 1997; Wilkinson & Boughman, 1998).

1.2. Learning versus genetic influence

When seeking evidence of similarity and convergence, a main issue is to check whether vocal matching between individuals can simply be a consequence of genetic proximity. Vocal production is strongly affected by genetic inheritance (Hammerschmidt & Fischer, 2008), as indicated by hybridization or cross-fostering experiments (Geissmann, 1984; Owren et al., 1993). A study in mandrills (*Mandrillus sphinx*) showed that the acoustic structure of contact calls was more similar between relatives than among unrelated individuals, and this similarity was likely due both to genetic relatedness and vocal copying (Levréro et al., 2015).

While the general structure of a call may be inherited, fine acoustic components may be influenced by the environment. As an example, the arch structure of contact calls appears genetically determined in rhesus macaques (*Macaca mulatta*; Owren et al., 1993), but the duration and amplitude of the frequency modulation, as measured in Japanese macaques, vary significantly from one context to another in any given individual (Koda, 2004). Another study on rhesus macaques showed closer similarities between the contact calls of females belonging to the same social group and matriline than those emitted by females from different social groups and matriline, yet the authors did not find any evidence of an effect of the degree of genetic relatedness, and concluded that similarities in vocal structures between individuals was a consequence of familiarity between them (Pfefferle et al., 2016). Likewise, the authors of three other studies also argued that acoustic

similarity in contact calls was not related to genetic relatedness (Japanese macaques: Tanaka et al., 2006; Campbell's monkeys: Lemasson et al., 2011; bonobos: Levréro et al., 2019).

1.3. Aims of the study

The present study aimed to investigate the effect of group membership, kinship and social relationships on vocal similarity in macaques. Wide cross-species variation in the social style of macaques makes it possible to assess the influence of dominance and kinship on vocal similarity, and thus evaluate the role played by the social environment in the evolution of communicative abilities (Freeberg et al., 2012; Gustison et al., 2012; Maciej et al., 2013). All macaques form linear hierarchies and live in groups that are structured in matriline, i.e., subgroups of relatives that are linked by maternal descent (Thierry, 2011). Species such as rhesus and Japanese macaques are characterized by strong social intolerance, meaning that they display a steep gradient of dominance coupled with conspicuous submission signals, and a strong preference for kin partners. Other species, like Tonkean macaques (*Macaca tonkeana*), show higher levels of tolerance, which corresponds to moderate power asymmetries, a high propensity to regulate conflicts through affiliative behaviours, and a low degree of nepotism (Thierry, 2007; Balasubramaniam et al., 2012; Rebout et al., 2017). The covariation hypothesis states that the different patterns of social styles are interconnected, and that any significant variation of a single character can induce a set of correlated changes in other traits (Thierry, 2007). We can therefore expect the influence of dominance and kinship on vocal similarity to be modulated by cross-species variations in social style.

We focused on contact calls, or 'coos'. In macaques these close-range vocalizations are mainly used to locate group members and maintain vocal contact between them, and they have a tonal acoustic structure in which the fundamental frequency is generally the dominant element. We analysed the inter-individual acoustic variation of coos emitted by females in rhesus and Tonkean macaques to test the following predictions: (1) Vocal similarity should be higher between individuals linked by group membership, close kinship and/or tight affiliative bonds than between individuals not having such links, (2) The effect of kinship and dominance relationships on vocal similarity should be more pronounced in rhesus macaques than in Tonkean macaques.

2. Methods

2.1. Subjects

Behavioural observations and acoustic recordings were carried out in 13 adult females from four groups of Tonkean macaques, and 12 adult females from two groups of rhesus macaques. All females were at least five years old, captive born, and had known maternal kin relationships.

Tonkean macaques belonged to a population originating from a stock imported to France in 1972, and since divided into several groups throughout the years (Table 1) (Herrenschmidt, 1977; Thierry et al., 1994). Tonkean group B consisted of 15 individuals including 4 adult females and was housed in a 120 m², 4 m high enclosure at the Orangerie Zoo of Strasbourg, France. The other three Tonkean groups (C, D, E) were housed in enclosures approximately 500 m² and 5 m high at the Parco Faunistico di Piano dell'Abatino Rescue Centre in Rieti, Italy (De Marco et al., 2014). These groups consisted of 16, 15 and 9 individuals including 4, 3 and 2 adult females, respectively (Table 1).

Rhesus macaques belonged to a population originating from a stock imported from India to The Netherlands in the seventies (Neefe et al., 1975; Doxiadis et al., 2013). The two groups of rhesus macaques were founded in 2004. They were housed in enclosures approximately 210 m² and 3 m high at the Biomedical Primate Research Center in Rijswijk, The Netherlands. They were composed of 35 and 31 individuals including 10 and 6 adult females, respectively (Table 1).

All enclosures were furnished with wooden structures, perches and ropes. Animals were fed commercial monkey diet pellets, complemented with fresh fruit and vegetables. Water was available *ad libitum*. This study respected the legal requirements and guidelines of the Italian, French and Dutch governments, and followed ASAB/ABS guidelines for the treatment of animals in behavioural research.

2.2. Data collection

We carried out observations in outdoor enclosures between 09:30 and 16:30 from September 2014 to May 2016 in Tonkean macaque groups, and from July 2016 to October 2016 in rhesus macaque groups (Table 1). We used random focal samples to record vocalisations (including coos) in adult females. Sample duration was 15 min in rhesus groups and Tonkean group B, and

Table 1.

Information about groups and subjects.

Group	Dates of group foundation and study	Composition of group ¹	Name and age in years of focal females ²	Percentage of maternal relatedness between focal females ³
Rhesus group A	founded in 2004 studied in July–October 2016	10 adult females, 3 adult males, 22 immatures	Pip (14), But (13), Isa (11), Nil (10), Hoe (10), Wie (9), Lok (7), Aus (6), Mon (5), Pan (5)	43%
Rhesus group B	founded in 2004 studied in July–October 2016	6 adult females, 1 adult male, 24 immatures	Tro (13), Plo (12), Hat (10), Jah (8), Kwe (7), Ymi (6)	27%
Tonkean group B	founded in 1978 studied in February–May 2016	4 adult females, 6 adult males, 5 immatures	Gil (27), Gai (9), Giu (9), Lis (5)	33%
Tonkean group C	founded in 2005 studied in September–December 2014	4 adult females, 4 adult males, 8 immatures	Pal (13), Sop (11), Pam (8), Pap (6)	50%
Tonkean group D	founded in 2007 studied in March–May 2015	3 adult females, 5 adult males, 7 immatures	Sib (12), Tet (11), Tan (11)	0%
Tonkean group E	founded in 2009 studied in September–December 2014	2 adult females, 3 adult males, 5 immatures	Nin (15), Nif (9)	100%

¹Immature: less than 5-year, adult: at least 5-year old (De Marco et al., 2014).

²Age at the beginning of data collection.

³Percentage of maternal relatedness (mother–daughter, sister–sister) between females calculated on the total number of relationships between females.

10 min in Tonkean groups C, D and E. This resulted in 12.7 ± 0.7 h of focal sampling per subject in rhesus macaques (total 203.25 h) and 13.6 ± 3.2 h in Tonkean macaques (total 177.4 h). We also recorded instantaneous samples of contact sitting and social grooming every 10 min.

Observers also used all occurrences sampling to collect data for supplantations (an individual approaches another who leaves immediately) and unidirectional conflicts (an individual threatens or attacks another who flees or submits) in the studied groups. As the majority of conflicts in Tonkean macaques were bidirectional, we collected additional data about agonistic interactions during competition tests in this species (see Thierry et al., 1994). According to breeding conditions, we recorded all occurrences of supplantations and unidirectional conflicts during food distribution in groups C, D and E (20-min periods every morning before the focal sampling), or around a single source of orange juice in group B (seven 2-h tests) (see Thierry et al., 1994).

Recordings of vocalizations were made with a Marantz (Eindhoven, The Netherlands) PMD 661 recorder (WAV format, sampling frequency: 44 100 Hz, resolution: 16 bits) and a Sennheiser (Wedermark, Germany) K6 & ME66 directional microphone. A lavalier microphone (TCM 160, Meditec, Singapore) was connected to the recorder to add comments about the context of call emission. To ensure emitter identification and sound quality, only coos emitted by individuals located within 5 m of the recorder were considered for analysis. Audacity software (version 2.0.5) was used to split the recordings for each coo, thus creating separate audio files to analyse calls. Records were of poor quality for one female (Isa) in rhesus macaques and they were removed from the analysis. Sampling produced an average of 14.5 ± 11.6 calls with good acoustic quality per female (Tonkean macaques: 15 ± 9.9 calls; rhesus macaques: 14 ± 13.7 calls).

2.3. Acoustic analysis

We applied the ANA software (Richard, 1991) to calculate a dyadic acoustic similarity index that expresses the degree of similarity of two given calls. Spectrograms were drawn with a Fast-Fourier Transformation using a window size of 256 and an overlap of 128. Recordings were downsampled at 11 025 Hz. A single investigator who had not been informed about the hypotheses underpinning the study, computed the similarity index for each pair of calls made by two different females. This index compares the shape of the frequency modulations of two calls, based solely on the patterns of the fundamental frequency (for other applications of this method in guenons, gibbons and macaques, see Lemasson et al., 2011, 2016; Candiotti et al., 2012; Koda et al., 2013). Every call emitted by a female was matched with

every call emitted by all other females. Given the frequency modulation pattern of macaques' coo calls, this procedure allows the computation of a single global similarity index rather than making a relatively subjective selection of specific acoustic parameters that are not always representative of the overall acoustic complexity. In a first step, the amplitude of all the sampled calls was homogenised; all calls were automatically boosted to the same maximum in a proportional way to ensure comparable amplitude scales and prevent any potential bias due to differences in recording quality. We then extracted the fundamental frequency to discard background noise and harmonics. In a third step, we ran an automatic calculation, based on pixel by pixel comparisons between spectrograms. Each pixel was associated with a grey value ranging from 0 (white) to 255 (full black). If one or both compared pixels had a grey value of zero, we attributed a score of 0. If the grey values of the two compared pixels differed by less than 16, we attributed a score of 2. We attributed a score of 1 to other combinations. (The choice to set the threshold at 16 was admittedly somewhat arbitrary at the outset. However, the validity of this choice was subsequently confirmed in all comparable published works with a broad range of non-human primate species including macaques (Lemasson et al., 2011, 2016; Candiotti et al., 2012; Koda et al., 2013), so this threshold was retained.) We computed a similarity index ranging between 0 and 1 by dividing the total of all scores by the total number of pixels in both spectrograms. The algorithm then carried out the same operation for all possible superpositions by comparing spectrograms of two individuals along the time axis. This generated similarity indices for every possible superposition (Lemasson et al., 2011). Once all possible superpositions had been compared, the algorithm determined the highest similarity index for the two spectrograms. Examples of comparisons are illustrated in Figure 1.

2.4. Assessment of kinship and social relationships

We assessed kinship based on the coefficient of maternal relatedness, computed from the pedigree data for each pair of subjects. Pairs were labelled as closely related when they involved sisters or mother/daughter, or distantly related when no such ties were involved (see Table 1). In a first step, we assessed the strength of the affiliative bond in each pair of group members by dividing the number of instantaneous samples involving an affiliative contact (social grooming, contact sitting) between partners by the total number of instantaneous samples. In a second step, we attributed pairs to two categories

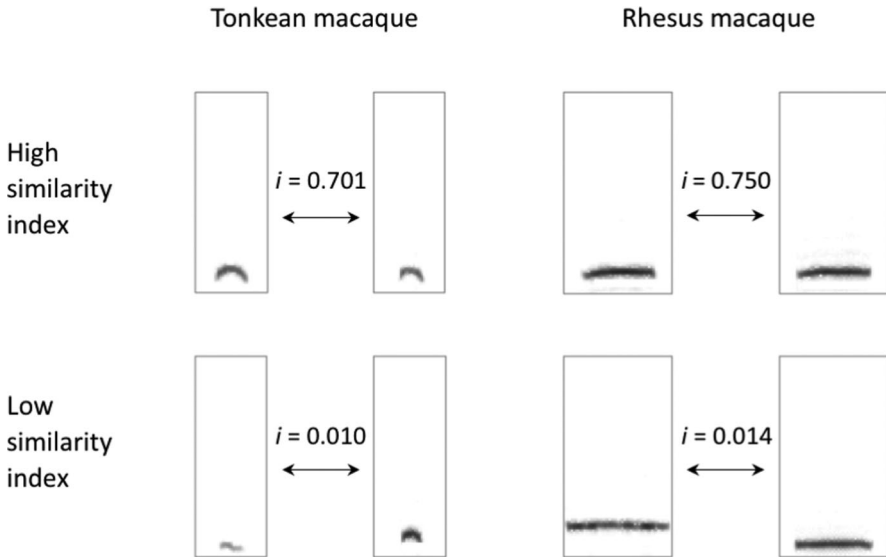


Figure 1. Examples of spectrograms (frequency as a function of time): two-by-two comparison of coos from different individuals and corresponding dyadic acoustic similarity indices i in Tonkean and rhesus macaques.

of equivalent size, *tightly* and *loosely affiliated*, according to bond strength values.

We assessed the dominance ranks of individuals in each group using supplantations and unidirectional conflicts. We applied SOCPROG software (Whitehead, 2009) to matrices built from agonistic interactions to rank individuals (excluding those less than 1-yr old as dominance rank is meaningless for them) in group dominance hierarchies. The linearity of hierarchies in all groups was verified using the linearity index h' (de Vries et al., 1993), with the following results: Tonkean group B: $h' = 0.51$, $p = 0.004$, Tonkean group C: $h' = 0.77$, $p < 0.001$; Tonkean group D: $h' = 0.64$, $p < 0.001$; Tonkean group E: $h' = 1$, $p = 0.023$; rhesus group A: $h' = 0.35$, $p = 0.003$; rhesus group B: $h' = 0.25$, $p = 0.030$). Individuals could then be attributed to three dominance categories (high-, medium- and low-rank) containing an equivalent number of group members, and we calculated a dominance delta for each pair of subjects: $\Delta = 0$, same dominance category; $\Delta = 1$, difference of one dominance category; $\Delta = 2$, difference of two dominance categories.

2.5. Statistical analyses

We performed Linear Mixed Models (LMM) using R 3.4.0 (R Core Team, 2017) and the package *lme4* (Bates et al., 2015) to test the effect of social factors on the inter-individual acoustic similarity of coos. The identity of focal females was included as a random factor. As groups of Tonkean and rhesus macaques differed in size, pairwise comparisons of inter-individual acoustic similarity indices resulted in an unbalanced dataset and thus precluded direct cross-species comparisons using statistical interactions. We therefore ran separate models for each species.

We first built models focusing on the effect of group and kinship in each species. The target variable was the dyadic acoustic similarity index. Predictor variables were the group (same vs. different group) and maternal relatedness (closely vs. distantly related); the age difference between females was also included due to its possible effect on acoustic variability (Ey et al., 2007). We then built models focusing on the effect of social relationships: dominance and affiliative bonds. The target variable was the similarity index. Predictor variables were the dominance delta (0, 1 or 2), affiliative bonds (tight vs. loose pairs), and the age difference between females. Maternal relatedness was also included as a random factor in the later models to control for a possible interaction with the dominance delta.

We checked that there was no significant collinearity between predictor variables (variance inflation factor below 3 for all variables). Because several predictor variables could influence target variables, candidate sets of models were evaluated using an information-theoretic approach. Suitable predictors were selected, then the *model.avg* function of the package *MuMIn* (Barton, 2016) was used to investigate their different combinations (Burnham & Anderson, 2002). The level of support was determined for each model through second-order Akaike's Information Criterion (AICc). We applied the procedure of Burnham & Anderson (2002) to define a 95% confidence set of model candidates: we summed the Akaike weights from the largest to the smallest until their sum was equal to or just above 0.95; candidate models were those with a weight sum below 0.95, plus the first model that attained or exceeded 0.95 (Burnham & Anderson, 2002: p. 169). When the confidence set contained more than one candidate model, the model with the largest number of variables was retained as the best one since it was the most explicative model. Residuals were checked visually for normality and homoscedasticity using the package *RVAideMemoire* (Hervé, 2017). Once the best-fitting

models had been identified, we determined the significance of effects with the Student's test provided by the package *lme4* (Bates et al., 2015). Post-hoc analyses based on Tukey corrections were run using the package *multcomp* (Hothorn et al., 2008) to assess the effects of factors with more than two conditions. Mean values and standard deviations were estimated for the different factor conditions using the package *effect* (Fox, 2003). The R script is provided in the Appendix in the online version of this journal, that can be accessed via brill.com/beh.

3. Results

3.1. Effect of group and kinship

In Tonkean macaques, the confidence set for the best model candidates contained a single model which included group and kinship variables. (Table 2, Tonkean model 1). Student's tests revealed that females belonging to the same group had higher similarity indexes than those of females in different groups (same group: estimated mean \pm SD = 0.276 ± 0.015 , different groups: 0.263 ± 0.015 , estimate_{same vs. different} \pm SE = 0.013 ± 0.003 , $t = 4.67$, $p < 0.001$), and that females that had a close kinship relation had a higher acoustic similarity index than others (closely related: 0.284 ± 0.015 , distantly related: 0.264 ± 0.015 , estimate_{close vs. distant} \pm SE = 0.020 ± 0.005 , $t = 4.30$, $p < 0.001$) (Figure 2).

The confidence set for rhesus macaques contained a single model which included age and kinship difference variables (Table 2, rhesus model 1). Student's tests showed that the acoustic similarity index decreased as the age difference between females increased (estimate \pm SE = -0.003 ± 0.0002 , $t = -13.1$, $p < 0.001$). They also revealed that females that had a close kinship relation had a higher similarity index than females with more distant relationships (closely related: 0.303 ± 0.016 , distantly related: 0.273 ± 0.016 , estimate_{close vs. distant} \pm SE = 0.030 ± 0.002 , $t = 16.7$, $p < 0.001$) (Figure 2).

The effect of kinship, calculated from the ratio between estimate of effect and intercept in the model, was equal to 0.074 in Tonkean macaques and 0.104 in rhesus macaques.

3.2. Effect of dominance and affiliative bonds

In Tonkean macaques, the confidence set contained a single model. This was the null model, and was not investigated further (Table 3, Tonkean model 1).

Table 2. Linear mixed models for group and kinship in Tonkean and rhesus macaques, ranked by the Akaike Information Criterion (AICc): estimates for quantitative effects, presence (+) for qualitative effects, and AICc computations.

Model	Group	Kinship	Age difference	Intercept	df	logLik	AICc	Delta	Weight	Weight sum
Tonkean macaques										
Model 1	+	+		0.261	6	10 323.4	-20 634.7	0	0.967	0.967
Model 2	+			0.273	5	10 318.6	-20 627.2	7.55	0.022	0.989
Rhesus macaques										
Model 1		+	-0.003	0.288	6	23 184.5	-46 357.1	0	0.998	0.998
Model 2	+	+	-0.003	0.287	7	23 179.5	-46 344.9	12.15	0.002	1

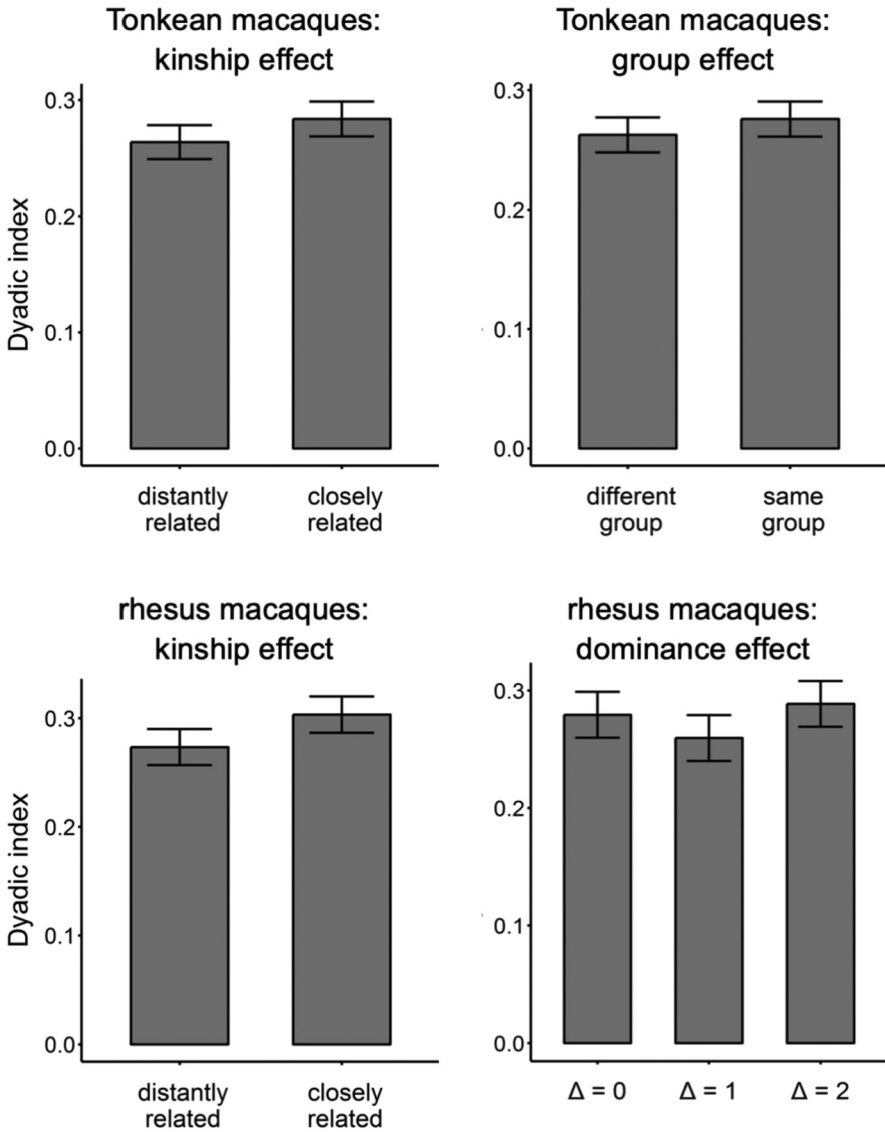


Figure 2. Results of linear mixed models: kinship and group effects in Tonkean macaques; kinship and dominance effects in rhesus macaques (means and standard deviations).

In rhesus macaques, the confidence set contained two models, and the best model included the dominance delta (Table 3, rhesus model 1). Post-hoc tests revealed that females that differed by two dominance categories ($\Delta = 2$)

($\Delta = 2$: 0.289 ± 0.019 , $\Delta = 0$: 0.279 ± 0.019 , i.e. high- and low-rank) had a higher similarity index than dyads from the same dominance category ($\Delta = 0$) (estimate _{$\Delta=2$ vs. $\Delta=0$} \pm SE = 0.009 ± 0.003 , $t = 3.49$, $p = 0.001$) or dyads that differed by one dominance category ($\Delta = 1$) ($\Delta = 2$: 0.289 ± 0.019 , $\Delta = 1$: 0.260 ± 0.020 , estimate _{$\Delta=2$ vs. $\Delta=1$} \pm SE = 0.029 ± 0.007 , $t = 4.19$, $p < 0.001$). Females belonging to the same dominance category ($\Delta = 0$) had a higher index than females that differed by one dominance category ($\Delta = 1$) ($\Delta = 1$: 0.260 ± 0.020 , $\Delta = 0$: 0.279 ± 0.019 , estimate _{$\Delta=1$ vs. $\Delta=0$} \pm SE = -0.020 ± 0.007 , $t = -2.98$, $p = 0.007$) (Figure 2).

4. Discussion

Results show that close kinship promoted vocal similarity between adult females in Tonkean and rhesus macaques. Moreover, vocal similarity was affected by group membership in Tonkean macaques but not in rhesus macaques, and also by inter-individual differences in dominance ranks in rhesus macaques but not in Tonkean macaques. This reveals the role played by species-specific social style in the structure of contact calls.

As predicted, close kinship ties promoted vocal similarity in the contact calls of females: sisters and mothers-daughters resembled one another more than other females in both species. Kinship is a basic tenet of macaque social organization, and although the degree of nepotism varies according to species, all macaque societies are organized along strong matrilineal lines (Thierry, 2010). By contrast, nepotism is less marked in guenons, as seen in female Campbell's monkeys and, correspondingly, no effect of kinship on the acoustic structure of their contact calls has been reported in this species (Lemasson & Hausberger, 2004). It should be added that we did not find any significant effect of affiliative bonds on acoustic similarity. As the number of adult females in each of the studied groups was limited, it may be that many of them were able to maintain good social relationships, making it impossible for us to appreciate the role of social affinities in vocal production. Note that the number of females in the study groups was comparable to those found for macaques in the wild (e.g., Edwin & Chopra, 1984; Pombo et al., 2004; Riley, 2007; Kumar et al., 2013). We additionally found that coos were more similar within groups than between them in Tonkean macaques. A number of studies have reported variations in primate vocalizations at the population

Table 3. Linear mixed models for dominance and affiliative bonds in Tonkean and rhesus macaques, ranked by the Akaike Information Criterion (AICc): estimates for quantitative effects, presence (+) for qualitative effects, and AICc computations.

Model	Dominance delta	Affiliative bond	Age difference	Intercept	df	logLik	AICc	Delta	Weight	Weight sum
Tonkean macaques										
Model 1				0.300	5	2267.5	-4525.0	0	0.981	0.981
Model 2		+		0.301	6	2264.3	-4516.5	8.41	0.015	0.996
Rhesus macaques										
Model 1	+			0.279	7	10819.3	-21624.6	0	0.559	0.559
Model 2				0.274	5	10817.0	-21624.0	0.51	0.425	0.984
Model 3		+		0.271	6	10814.5	-21617.0	7.60	0.012	0.996

level (see Introduction), but few have reported an effect of group membership on acoustic similarity among non-human primates (Crockford et al., 2004; Tanaka et al., 2006).

As in other studies, it is difficult to disentangle the experiential and/or genetic factors responsible for the effects of kinship and group membership. It is possible that the resemblance between close relatives had some genetic basis. Although the occurrence of genetic drift is unlikely across a small number of generations, a founder effect cannot be excluded. However, previous studies did not find an effect of genetic inheritance on the fine acoustic components of coos (Lemasson & Hausberger, 2004; Lemasson et al., 2006, 2016) which are more likely influenced by social patterns. It is known that learning can contribute to vocal convergence (Tanaka et al., 2006; Lemasson et al., 2011; Levréro et al., 2015; Pfefferle et al., 2016). Following the merging of individuals, some vocalizations of group- or pair-members came to converge within a period as short as three years in chimpanzees (food grunts: Watson et al., 2015), or even months or weeks in Campbell's monkeys (agonistic, affiliative & contact calls: Lemasson & Hausberger, 2004) and pygmy marmosets (trills: Snowdon & Elowson, 1999). Most of the macaque groups in the present study were founded relatively recently, and vocal copying between individuals may explain a substantial part of the membership effect found in the acoustic structure of female coos.

In rhesus macaques, the vocal similarity of contact calls was influenced by the position of females in the social hierarchy: the coos emitted by partners displaying a strong dominance asymmetry exhibited more similarity than those of females with less dominance difference. This is consistent with the results of a previous study in another intolerant species, the Japanese macaque, which led the authors to assume that subordinate females tend to converge with the voices of leaders (Lemasson et al., 2016). In rhesus macaques, however, the coos of females belonging to the same dominance category also appeared to be more similar than those of females that differed by one dominance category. This can be considered a case of convergence where the development of vocal similarity would be favoured by the low levels of social competition between these individuals and between those that are separated by strong differences in dominance ranks, whereas it would be hindered by heightened competition between group members with closer dominance ranks (see Belzung & Anderson, 1986). Further research will be needed to pinpoint the origin of this non-linear effect of female dominance

status. It is noteworthy however that this effect cannot be explained by mere genetic inheritance, reinforcing the argument that social relationships influence the acoustic structure of coos.

Contrary to results in rhesus and Japanese macaques (Lemasson et al., 2016), testing the effect of dominance categories on the acoustic similarity of female coos did not yield any significant effect in Tonkean macaques. This result is in accordance with the social style of this species. Whereas rhesus and Japanese macaques display strong power asymmetries between individuals, Tonkean macaques are characterized by relaxed dominance relationships. Interestingly, a similar result was found for the chorused calls of subordinate male chimpanzees, which did not resemble the calls produced by the top-ranking male of their community (Mitani & Gros-Louis, 1998). The societies of this species can be considered tolerant when compared to the range of social styles reported in macaques (de Waal, 1986; Silk et al., 2013; Rebout et al., 2017). As for the effect of kinship on acoustic similarity, the dependence of vocal similarity on the dominance system of the species lends support to other evidence indicating that patterns of communication covary with patterns of social organization (Dobson, 2012; Freeberg et al., 2012). Moreover, a stronger effect of kinship on vocal similarity in rhesus macaques, linked to a higher degree of closure of matrilineal groups compared to Tonkean macaques, may explain that we did not find an effect of group membership in the former species. In other words, open social relationships would favour acoustic similarity at group scale in tolerant species, whereas similarity would rather occur between individuals belonging to same subgroups in more nepotistic species.

It has been suggested that vocal convergence promotes group cohesion and the identification of group members (Giles et al., 1991; Snowdon & Hausberger, 1997; Wilkinson & Boughman, 1998; Candiotti et al., 2012). It could also be that the variations observed between conspecifics are non-adaptive consequences of genetic divergence and/or individual learning abilities (Thierry, 1994). Differences between calls emitted by different categories of females did indeed remain subtle. The search for limited variations in behaviours and vocalizations often provides evidence of inter-group differences in non-human primates (e.g., Crockford et al., 2004; Tanaka et al., 2006; Nakagawa et al., 2015), which may prove to be a general phenomenon among primates.

Although no one disputes the fact that humans have far greater control over their vocal production apparatus, a certain degree of volitional control in vocal production has however been recently reported in some Old and New World monkeys and apes. For instance, gibbons can be conditioned to vocalise on command (Koda et al., 2007), they voluntarily perform a precise tuning of frequencies when singing in a helium chamber (Koda et al., 2012), and orang-utans (*Pongo* sp.) can instantaneously match human-produced sounds as they are randomly modulated in pitch (Lameira et al., 2016). Some recent neurobiological studies suggested the existence in non-human primates of a cognitive neuronal network capable of taking control over a basic vocal motor network that produces largely innate vocal utterances but lacks the ability to learn or imitate new vocal signals (Hage et al., 2013; Ackermann et al., 2014; Hage, 2018). These studies also suggested the importance of auditory feedback — notably from family members — on this cognitive vocal motor control; they pointed to a possible role of audio-vocal networks and cortico-basal loops in experience-dependent modifications of the acoustic call structure during vocal development in non-human primates (Hage, 2018). However, it appears important to distinguish vocal flexibility in the production of innate vocalizations — as shown in both monkeys and apes (Lemasson et al., 2011; Watson et al., 2015) — from vocal flexibility in the production of new vocalizations beyond the species innate repertoire — as found in apes only (Hopkins et al., 2007; Lameira et al., 2013). Belyk & Brown (2017) proposed an alternative scenario where voluntary control of the vocal apparatus and vocal production learning co-evolved with a progressive modification of brain morphology throughout the audiovisual system across primate orders. They suggested a neurophenotypic continuum from monkeys to great apes to humans. The issue is still debated. With regard to macaques, our findings support a more finely-tuned control than previously expected, and are in line with previous works showing that female Japanese macaques can modify the fundamental frequency pattern of their calls — namely duration and amplitude of frequency modulation — to attract attention from others (Koda, 2004), and are thus at least capable of controlling both their airflow and vocal fold oscillation in a limited but perceptible way.

The present results highlight the flexibility of vocal communication in primates like macaques and underline the influence of social style on this ability. The investigation should now be extended to other types of vocalizations in further groups and species to assess the generality of our conclusions, and

must include playback experiments that aim to study the functional significance of the variation evidenced here.

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Appendix: R script

```

####packages downloading####
library(lme4)
library(MuMIn)
options(na.action=na.fail)
library(beepR)
library(RVAideMemoire)
library(lsmeans)
library(multcomp)

####function vif.mer####
vif.mer <- function (fit) {
  ## adapted from rms::vif

  v <- vcov(fit)
  nam <- names(fixef(fit))

  ## exclude intercepts
  ns <- sum(1 * (nam == "Intercept" | nam == "(Intercept)"))
  if (ns > 0) {
    v <- v[-(1:ns), -(1:ns), drop = FALSE]
    nam <- nam[-(1:ns)]
  }

  d <- diag(v)^0.5
  v <- diag(solve(v/(d %o% d)))
  names(v) <- nam
  v
}

#####part 1 Tonkean macaques#####

Data_T_gp_kin <-
read.table("C:/Users/user/Documents/Data_T_gp_kin.csv",header=TRUE, sep=";",
na.strings="NA", dec=".", strip.white=TRUE)

tonk<- lmer(index ~ group + age_difference + kinship +(1|indiv_call1) +
(1|indiv_call2), data = Data_T_gp_kin)
vif.mer(tonk)
summary(tonk)

dre<-dredge(tonk)
dre
summary(model.avg(dre))

besttonk<- lmer(index ~ group + kinship +(1|indiv_call1) + (1|indiv_call2), data
= Data_T_gp_kin)
summary(besttonk)

plotresid(besttonk)

cht <- glht(besttonk, linfct = mcp(kinship = "Tukey"))
summary(cht)
cht <- glht(besttonk, linfct = mcp(group = "Tukey"))
summary(cht)

#####part 1 rhesus macaques#####

Data_R_gp_kin <-
read.table("C:/Users/user/Documents/Data_R_gp_kin.csv",header=TRUE, sep=";",
na.strings="NA", dec=".", strip.white=TRUE)

rhes<- lmer(index ~ group + age_difference + kinship +(1|indiv_call1) +
(1|indiv_call2), data = Data_R_gp_kin)

```

```

vif.mer(rhes)
summary(rhes)
dre<-dredge(rhes)
dre
summary(model.avg(dre))

rhes<- lmer(index ~ group + kinship + age_difference + (1|indiv_call1) +
(1|indiv_call2), data = Data_R_gp_kin)
summary(rhes)

plotresid(rhes)

cht <- glht(rhes, linfct = mcp(kinship = "Tukey"))
summary(cht)
cht <- glht(rhes, linfct = mcp(group = "Tukey"))
summary(cht)

#####part 2 Tonkean macaques#####

Data_T_d_a <- read.table("C:/Users/user/Documents/Data_T_d_a.csv",header=TRUE,
sep=";", na.strings="NA", dec=".", strip.white=TRUE)

Tonk <- lmer(index ~ dominance + affiliative_bond + age_difference +
(1|indiv_call1) + (1|indiv_call2), data = Data_T_d_a)
vif.mer(Tonk)
summary(Tonk)

dre<-dredge(Tonk)
dre
summary(model.avg(dre))

#####part 2 rhesus macaques#####

Data_R_d_a <- read.table("C:/Users/user/Documents/Data_R_d_a.csv",header=TRUE,
sep=";", na.strings="NA", dec=".", strip.white=TRUE)

rhes <- lmer(index ~ dominance + affiliative_bond + age_difference +
(1|indiv_call1) + (1|indiv_call2), data = Data_R_d_a)
vif.mer(rhes)
summary(rhes)

dre<-dredge(rhes)
dre
summary(model.avg(dre))

bestrhes <- lmer(indice ~ dominance + (1|indiv_call1) + (1|indiv_call2), data =
Data_R_d_a)
summary(bestrhes)

plotresid(bestrhes)

cht <- glht(bestrhes, linfct = mcp(dominance = "Tukey"))
summary(cht)

```