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Vocal accommodation in bonobos

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Dialects and accents in human speech have a demonstrated social function as markers of group identity and often serve as psychological foundations of trust and cooperation. The extent to which this phenomenon is a feature of primate communication more generally is still debated. Here, we show that the vocal signatures of bonobos, *Pan paniscus*, belonging to three social groups show group-specific acoustic features independent of genetic relatedness. We compared the barks of 22 adults from the three groups and found that individuals currently living together had more similar barks than individuals that had never met or had lost touch with each other, regardless of their degree of genetic relatedness. We concluded that group-specific vocal accommodation is present in bonobos, suggesting an early evolutionary emergence of vocal plasticity in apes, which could be a means to signal social closeness between individuals.

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In human social groups, individuals evaluate the social proximity, life history and personality of speakers based on a set of vocal features, such as pitch, formant frequencies, intonation or speed of speech (e.g. Bradac, 1990; Scherer, 1979; see Bernhold & Giles, 2020; Ruch et al., 2018, for reviews). Vocal features are also used to determine group membership, to the effect that speakers with the same accents or dialects are rated as more valuable and trustworthy than individuals with foreign accents or dialects (Fuertes et al., 2011; Shah, 2019). This psychological predisposition may also explain why individuals who immigrate into other social groups gradually accommodate the acoustic features specific to their new hosts (e.g. Pardo et al., 2012, 2013), which presupposes some degree of vocal flexibility (e.g. Janik & Knornschild, 2021; Pickering & Garrod, 2013; Prinz & Neumann, 1990; Pulvermüller & Fadiga, 2010). A facilitating element in vocal accommodation is, of course, the human capacity for vocal learning from infancy to adulthood (Fitch et al., 2002).

Vocal accommodation can be indeed considered a form of vocal learning; that is, the modification of vocal signals as a result of exposure to any external acoustic stimuli (broad definition from Janik & Slater, 2000). Songbirds (Passeriformes) are by far the most studied animals when it comes to vocal learning (Cate, 2021). Many birds learn to sing elements of song that are shared with other individuals in their geographical area, leading to vocal dialects (Marler & Tamura, 1962; Podos & Warren, 2007; Wright & Dahlin, 2017). These song elements are common within populations and are often stable over time, for example the trill segments of the white-crowned sparrow, *Zonotrichia leucophrys* (Nelson & Poesel, 2009; Nelson & Soha, 2004), or the buzz segment of the Savannah sparrow, *Passerculus sandwichensis* (Williams et al., 2019). However, there is a growing body of literature suggesting that some animals, for which there is no evidence of explicit vocal learning (e.g. producing a new song or call by modelling or imitation), are nevertheless capable of modifying their calls in response to the social environment. Evidence for such vocal accommodation in nonoscine birds is scarce compared to that for mammals. There is one report in a nonvocal learner bird, the penguin *Spheniscus demersus*, which showed that penguins vocally converged to their

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current colony partner (Baciadonna et al., 2022). Vocal accommodation in birds has also been demonstrated in response to noisy surroundings (e.g. increasing the loudness or singing higher-pitched notes in response to an increased background noise: Brumm & Zollinger, 2011; Hao et al., 2024; Ruch et al., 2018).

In mammals, short-term vocal accommodation appears to be fairly widespread (see Knörnschild, 2014; Ruch et al., 2018, for reviews), while long-term vocal accommodation to new social partners or groups has mainly been reported in bats and some nonhuman primates. For example, captive pygmy marmosets, *Cebuella pygmaea* (Snowdon & Elowson, 1999), and common marmosets, *Callithrix jacchus* (Zürcher et al., 2019), sound more similar several weeks after being paired, while in the wild there are population level signatures (pygmy marmosets: De La Torre & Snowdon, 2009; common marmosets: Zürcher & Burkart, 2017). Other evidence is from captive Campbell's monkeys, *Cercopithecus campbelli* (Lemasson & Hausberger, 2004), with vocal similarities reflecting social bonds (Lemasson et al., 2011). In great apes, the only published study is with chimpanzees, *Pan troglodytes*, showing that individuals transferred from one zoo to another gradually changed the acoustic structure of their food calls towards those of their new host group (Watson et al., 2015). However, the interpretation of these findings as a case of vocal accommodation has been challenged, as they could equally be explained as changes in arousal levels linked to the new social constellations (Fischer et al., 2015).

Overall, the standard interpretation of vocal accommodation effects, in animals and humans, is that it functions to strengthen social bonds within breeding pairs or social groups, and to signal group membership. However, this requires evidence that acoustic similarities are not the result of underlying genetic similarities translating, for example, into similar vocal tracts. To our knowledge, this hypothesis has been addressed in three primate species: Campbell's monkeys (Lemasson et al., 2011), mandrills, *Mandrillus sphinx* (Levréro et al., 2015), and Guinea baboons, *Papio papio* (Fisher et al., 2020), with inconclusive results. In Campbell's monkeys and Guinea baboons, vocal similarities could not be explained by genetics (but only with social closeness), while in mandrills both social and genetic factors explained part of the variance. However, quantifying the contribution of genetic relatedness in vocal features is notoriously difficult since it interacts with life history factors, which often precludes simplistic interpretations.

In the present study, we analysed a number of acoustic parameters of bonobo, *Pan paniscus*, bark vocalizations, comparing individuals for which we knew their complete life histories, kinship and social records. We carried out pairwise comparisons of vocal convergence, taking into account time spent living together and degree of genetic relatedness. In the wild, bonobos inhabit the forest and forest - savannah regions of the Democratic Republic of Congo (e.g. Fasbender et al., 2022; Takemoto, 2017) and live in complex female-dominated fission–fusion societies. Bonobos are highly vocal (Furuichi, 2011; Hohmann & Fruth, 1994, 2002; White, 1996) with several call types used in a range of contexts (e.g. Clay et al., 2015). Here, we focused on barks, a common loud call produced when discovering food and during feeding but also during agonistic and intercommunity encounters (Bermejo & Omedes, 1999). In captivity, feeding and agonistic interactions are also the main causes of production, such as when food is anticipated or in response to external disturbances (De Waal 1988; Keenan et al., 2020).

We tested whether individuals belonging to the same social group produced barks that were acoustically more similar relative to individuals from different groups. We also tested whether vocal similarity could partially be explained by genetic relatedness, based on the fact that genetically related individuals were more likely to have more similar vocal tract anatomies.

METHODS

Subjects

We collected vocal recordings from 22 adult bonobos (14 females and eight males older than 10 years; Behringer et al., 2014) from three distinct captive groups: Apenheul Primate Park, the Netherlands (six individuals); Planckendael Zoo, Belgium (six individuals); and La Vallée des Singes, France (10 individuals). Two of these individuals are wild-born bonobos, and the other 20 are descended from 17 other wild-born bonobos. To investigate the effects of genetic relatedness and social familiarity on vocal proximity, we considered dyads (pairs) of individuals. Each dyad (total number = 231) was characterized by the genetic relatedness between the two individuals considered, which was provided by the bonobo studbook manager of the European Association of Zoos and Aquariums. Paternity of all study subjects had been confirmed by analyses of microsatellites (Stevens, n.d.) and r ranging from 0 to 0.5. Each dyad was also characterized by the fact that the individuals were currently living in the same social group ($N = 75$ dyads), had lived in the same group in the past ($N = 25$) or had never lived together ($N = 131$). All bonobos in 'same group' dyads had been living together in the same zoo for at least 12 months. Individuals who were no longer living in the same group had been separated for 2 to 9 years.

Recordings

Recordings were collected between March 2013 and May 2014, from 0800 to 1800 hours (Apenheul Primate Park: approximately 175 h of recording; Planckendael Zoo: approximately 190 h of recording; La Vallée des Singes: approximately 115 h of recording). We used a Sennheiser MKH70-1 ultradirectional microphone (www.sennheiser.com) and a Zoom H4 digital recorder (zoomcorp.com) with a sampling rate of 44 100 Hz. All the recordings were performed at a distance of between approximately 5 m and 20 m, in open environments, which limits the impact of propagation on the quality of the recordings (Wahlberg & Larsen, 2017). Each individual was recorded several times (average number of recordings per individual: 20.4 ± 14.3 , range 5–55). We focused on a single type of call, the bark (Fig. 1a), which is a vocalization commonly uttered in a variety of contexts, both in captivity and in the wild (Bermejo & Omedes, 1999; Clay & Zuberbühler, 2009; De Waal, 1988; Keenan et al., 2020). Barks accounted for almost 20% of all recorded calls.

Acoustic Analysis

We analysed 431 calls (mean calls per individual = 20, range 5–55) considering the following 12 acoustic variables.

Six variables described the fundamental frequency (pitch) and its temporal modulation (manually measured using the Raven PRO 1.3 spectrogram, www.ravensoundsoftware.com, window size = 512): (1) F_0 Start (fundamental frequency at the beginning of the call, Hz); (2) F_0 End (fundamental frequency at the end of the call, Hz); (3) F_0 Maximum (highest frequency reached on the fundamental, Hz); (4) Call duration (s), (5) Slope-Start to Midpoint of F_0 (calculated as: F_0 at Midpoint of Call duration – F_0 Start/Time at Midpoint of Call duration); and (6) Slope-Midpoint to end of F_0 (calculated as: F_0 End – F_0 at Midpoint of Call duration/Time at Midpoint of Call duration).

Six variables described the energy distribution in the frequency spectrum (measured automatically using Raven PRO 1.3): (1) Q1 Frequency (the frequency of the spectrum corresponding to the first quartile (25%) of the energy of the frequency spectrum, Hz); (2)

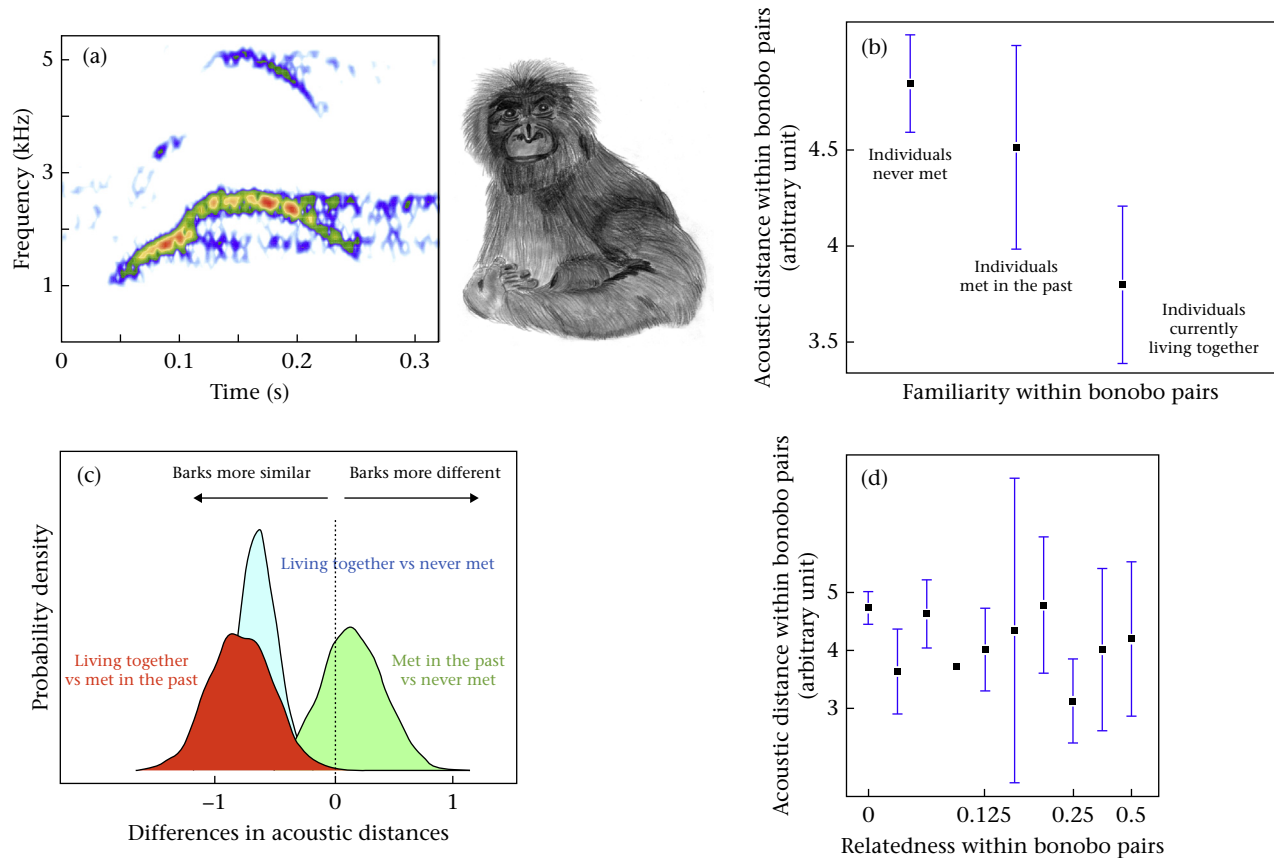


Figure 1. Vocal accommodation in bonobos. (a) Spectrogram of a bonobo's bark call (see Supplementary Material, audio file). (b) The acoustic distance between the barks of two bonobos in relation to familiarity. Solid markers represent medians of posterior distributions, with bars indicating the 95% credible intervals. (c) The difference in acoustic distance between barks of two bonobos that live together ($N = 75$ pairs) compared to those of bonobos that have lived together in the past ($N = 25$) or have never met ($N = 131$). (d) The acoustic distance between barks of two bonobos in relation to their degree of relatedness. Solid markers represent medians of posterior distributions, with bars indicating the 95% credible intervals. Bernard Mathevon drew the bonobo.

Q1 Time (the duration since the start of the call containing 25% of the spectral energy, s); (3) Q3 Frequency (the frequency of the spectrum corresponding to the third quartile (75%) of the energy of the frequency spectrum, Hz); (4) Q3 Time (the duration since the start of the call containing 75% of the spectral energy, s); (5) Maximum Frequency (the frequency at which the maximum energy occurs in the call spectrum, Hz); and (6) Maximum time (the first time point along the call where the maximum amplitude occurs on the waveform, s).

Measure of Vocal Proximity

For each bonobo, we first calculated the median value of each of the 12 acoustic variables considering all recorded calls (Supplementary Material, Table S1). We then standardized these values into z scores and performed a principal component analysis (PCA; Supplementary Material, Table S2). We retained the first five factors of the PCA, which accounted for over 90% of the total variance. For each pair of individuals ($N = 231$), we finally calculated the acoustic distance between pairs of individuals (Euclidean distances) in the PC1–PC5 acoustic space (Supplementary Material, Table S3). These distances served as a measure of vocal proximity, with smaller acoustic distances indicating greater acoustic similarity.

As individuals from one group are more likely to be recorded during the same social event than individuals from another group, we checked the independence of our recordings for individuals living in the same group ($N = 75$ pairs). We compared the date and

time of the vocal sequences from which their calls were extracted. Overall, 91.5% of these vocal sequences ($N = 1116/1220$) were recorded an hour or more apart, suggesting that the calls were not directly related. Of these sequences, 84.2% came from different days ($N = 940/1116$). Furthermore, the median of each acoustic parameter was calculated from several calls (range 5–55, depending on individuals), and an average of 92.0% of these calls within pairs came from vocal sequences recorded 1 h or more apart (range 66.7–100%, depending on pairs). We therefore assumed that the acoustic distance between individuals currently living in the same group or different groups could be compared without reflecting a particular social event effect.

Statistical Analyses

We tested whether genetic proximity and familiarity between the two individuals of each pair influence their acoustic proximity using a mixed Bayesian model (brms R package, cran.r-project.org/web/packages/brms/index.html). The acoustic distance within each pair of individuals was the outcome variable. Genetic relatedness (ranging from 0 to 0.5), familiarity (0 when the two individuals had never met, 1 if they had lived in the same social group in the past, or 2 if they currently lived together) and sex (female–female, male–male or female–male pair) were included in the model as fixed factors. Individual identity of each bonobo was included as a random factor (See Supplementary Material, Table S3, for details of relatedness and familiarity for each bonobo pair.). The structure of

the model in brms syntax was as follows: acoustic distance ~ relatedness + familiarity + sex + (1|identity of bonobo 1) + (1|identity of bonobo 2).

To test whether the similarity between barks of bonobos living in the same group may increase with time, we reran the analysis restricted to pairs of bonobos currently living together and using the following Bayesian model: acoustic distance ~ (log-number of months spent together) + relatedness + (1|identity of bonobo 1) + (1|identity of bonobo 2). The reported effects are medians of posterior distributions and 95% credible intervals (Bürkner, 2017; Kruschke, 2014).

In addition, we tested whether particular acoustic traits are likely to carry a social group vocal signature. As some of the acoustic variables measured are redundant, we focused on three variables from among those with the highest weight in the principal components (see Supplementary Material, Table S2) that describe different properties of the sound: the duration of the cry (temporal domain), the maximum frequency of the fundamental (frequency domain) and the slope of the fundamental frequency between the beginning and middle of the cry (frequency modulation domain). The Bayesian models followed the following syntax: acoustic variable ~ social group signature.

Ethical Note

All methods were carried out in accordance with the relevant French national guidelines and regulations, under the authorization of the Institutional Animal Ethical Committee of the University of Lyon/Saint-Etienne (No. 42-218-0901-38 SV 09). This study only involves spontaneous vocal recordings of animals in their natural social group and in their usual environment. No experimental protocols have been conducted in this study.

RESULTS

The acoustic similarity of barks produced by two bonobos living in the same group was greater than by two individuals that had never met each other before (Bayesian mixed model, difference in acoustic distance between calls: -0.66 , 95% CI $[-0.97, -0.35]$) or that had been together in the past (-0.80 , 95% CI $[-1.32, -0.27]$). On the other hand, the barks of bonobos that had lived together in the past were no more similar to each other than the barks of bonobos that had never met (0.15 , 95% CI $[-0.37, 0.68]$; Fig. 1b and c, Table 1; see Supplementary Table S3 for a comprehensive list of the acoustic distances within pairs of bonobos). Moreover, we found no effect of the degree of relatedness between individuals (95% CI $[-0.73, 0.54]$; Fig. 1d; Table 1). Similarly, we found no effect linked to the sexes of the individuals making up the dyads: the acoustic distance between two individuals of different sexes was neither significantly shorter nor significantly greater than the acoustic distance between two individuals of the same sex (male pair versus female–male pair: 0.66 , 95% CI $[-0.08, 1.44]$; female pair versus female–male pair: -0.50 , 95% CI $[-1.18, 0.19]$; female versus male pair: -1.15 , 95% CI $[-2.53, 0.17]$; Table 1).

When restricting the analysis to pairs of bonobos currently living together, we found no effect of the number of months spent together (-0.18 , 95% CI $[-0.60, 0.24]$; Table 2). As far as vocal signatures are concerned, none of the three acoustic variables considered (duration, maximum fundamental frequency and slope of the fundamental frequency) alone carried the signature of the social group (Table 3).

DISCUSSION

Our results showed that bonobos living in the same social group produced vocalizations with more similar acoustic characteristics

Table 1
Effect of genetic proximity, familiarity and sex on acoustic proximity within a bonobo pair

Predictors	Estimate	95% Credible interval	Rhat	Bulk ESS	Tail ESS
Intercept	5.0	4.17, 5.82	1.00	909	1691
Relatedness between the individuals composing the pair	-0.18	$-1.47, 1.09$	1.00	2918	2836
Familiarity between the individuals composing the pair					
Together in the past	0.17	$-0.37, 0.68$	1.00	2898	3080
Currently together	-0.66	$-0.97, -0.35$	1.00	3309	2936
Sexes of the individuals composing the pair					
Female–male	-0.50	$-1.18, 0.19$	1.01	915	1569
Male–male	-1.16	$-2.53, 0.17$	1.01	875	1358

Model syntax: acoustic distance ~ relatedness + familiarity + sex + (1|identity of bonobo 1) + (1|identity of bonobo 2). ESS: effective sample size.

Table 2
Effect of the time spent together on acoustic proximity within a pair of familiar bonobos

Covariate	Estimate	95% Credible interval	Rhat	ESS	Posterior distribution > 0
Intercept	4.90	2.45, 7.39	1.00	2010	2753
Number of months spent together	-0.18	$-0.60, 0.24$	1.00	2317	2807
Relatedness between the individuals composing the pair	0.51	$-1.83, 2.84$	1.00	2783	2868

Model syntax: acoustic distance ~ (log-number of months spent together) + relatedness + (1|identity of bonobo 1) + (1|identity of bonobo 2). ESS: effective sample size.

Table 3
Test of the importance of acoustic features for group vocal signatures

	Call duration	F ₀ max	Slope StarttoMid
Group A compared to group B	0.40, 95% CI $[-0.17, 0.92]$	0.05, 95% CI $[-0.68, 0.75]$	0.83, 95% CI $[-0.01, 1.71]$
Group A compared to group C	0.69, 95% CI $[0.18, 1.16]$	0.45, 95% CI $[-0.19, 1.05]$	0.16, 95% CI $[-0.55, 0.97]$
Group B compared to group C	0.29, 95% CI $[-0.14, 0.74]$	0.43, 95% CI $[-0.18, 1.02]$	-0.65 , 95% CI $[-1.36, 0.06]$

A = Apenheul; B = Planckendael; C = La Vallée des Singes; medians of posterior distributions and 95% credible intervals are shown.

than did bonobos living apart, controlling for the independence of recordings for ingroup individuals. Furthermore, and contrary to predictions, the degree of relatedness between two individuals did not impact on their vocal similarity. We concluded, from these findings, that bonobos showed vocal accommodation, mirroring previous findings with chimpanzee food calls (Watson et al., 2015).

The main strength of our study is to show bonobo vocal flexibility in a naturalistic context, without training (as recommended in Zuberbühler et al., 2022). The observed vocal accommodation is probably facilitated through social interactions (Sewall et al., 2016; Tyack, 2008), even though environmental effects cannot be completely discounted (e.g. Candiotti et al., 2012; Ey et al., 2009; Hotchkyn et al., 2015; Zhao et al., 2019). For example, the specific configuration of the enclosures at each zoo may result in specific acoustic characteristics of the recordings, leading to a group signature due to the physical environment rather than the social environment. While this hypothesis cannot be completely ruled out, the fact that we still found a group signature despite the fact that recordings were made from different indoor and outdoor locations in one zoo (La Vallée des Singes) suggests the existence of a group signature independent of location. It is plausible that changing vocal features to become more similar to the ones of social partners is positively reinforced one way or another (e.g. by facilitating social bonding as we observe in humans: see Ruch et al., 2018, for a review).

Contrary to our hypothesis, vocal similarity between two bonobos appears to be independent of their genetic proximity, a result already suggested in two other nonhuman primate species (Campbell's monkeys: Lemasson et al., 2011; Guinea baboons: Fischer et al., 2020). However, this pattern is not universally observed (e.g. mandrills: Levréro et al., 2015; rhesus macaques, *Macaca mulatta*: Rendall et al., 1996). In addition, the influence of familiarity and relatedness may vary depending on the function of the vocalization under study. Indeed, some vocalizations may be better candidates for vocal convergence between partners, whereas others are useful for individual identification and will experience limited plasticity (e.g. long-distance contact calls: Zürcher et al., 2021). In the present study, we focused on a single type of bonobo vocalization even though their vocal repertoire is extensive and varied. In a previous study, we found that individual identity is strongly encoded in calls made in high-arousal contexts, whereas it decreases in calls made in low-arousal contexts (Keenan et al., 2020). It is possible that the influence of genetics and familiarity on call structure varies within the gradation of bonobo calls.

A second limitation of our study is the relatively small amount of data. Few zoos house bonobos, and the translocation of bonobos between zoos is a complicated operation and a rare event. Given the constraints of our sample size, we took a conservative approach and did not investigate the potential impact of hierarchical rank on vocal accommodation. Bonobo social interactions are rich, and we know for instance that the social bonds between group members influence their rate of vocal exchanges, but their sex or rank do not (Levréro et al., 2019). Concerning the possible impact of individuals' sex on their ability to perform vocal accommodation, we evaluated one aspect by taking into account in the statistical models the fact that the dyads of individuals (for which acoustic distance is measured) were composed of individuals of either the same sex or the opposite sex. The results show that this sex-related characteristic of the dyad did not influence the acoustic distance between individuals. However, further research is needed to test whether vocal accommodation depends on sex and the social partnership between individuals.

Our study also suggests that bonobo calls carry a vocal signature of the social group, but it was not within the aims of the study to

explore its structure. However, we have shown that single acoustic descriptors are certainly not enough to define it, and that these signatures are probably multivariate. Testing whether and how bonobos can identify these signatures will require further investigation.

When evaluating the vocal signature of a social group, one possible bias is to analyse nonindependent recordings within each group. For example, if individuals from one group are systematically recorded in a high agonistic context and individuals from another group are systematically recorded in a low agonistic context, the acoustic structure of vocalizations will differ between the two groups without vocal accents being defined *sensu stricto*. In the present study, we have tried to limit this type of bias as much as possible by recording each individual several times, at different times and in different behavioural contexts (as described in the Methods). However, we cannot completely rule out the possibility that the social atmosphere differs from one group to another and that these differences may help to define particular group accents.

Our results suggest remarkable vocal plasticity in bonobos, as they exhibit the ability to acquire or lose local accents, as a function of social navigation throughout their life, a process somewhat similar to what is observed in humans (Reubold & Harrington, 2015). However, it is important to acknowledge that the extent of vocal modulation and the production of novel vocalizations in bonobos should not be overstated. Vocal accommodation entails subtle modifications in vocal output (Fisher et al., 2020; Ruch et al., 2018), which aligns with what we observed in the bark vocalizations of bonobos. The mechanisms underlying vocal accommodation still need to be explored but are possibly the result of auditory experience (Fischer et al., 2020; Mathevon, 2023; Ruch et al., 2018; Tyack, 2016). In conclusion, although this study represents the first demonstration that bonobos are capable of vocal accommodation and that this accommodation underlies the flexibility of their vocal production, our results do not drastically challenge the previous consensus about vocal learning in apes.

Author Contributions

Florence Levréro: Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization. **Jeroen M.G. Stevens:** Resources. **Klaus Zuberbühler:** Writing – original draft, Validation, Supervision. **Nicolas Mathevon:** Writing – review & editing, Writing – original draft, Formal analysis. **Sumir Keenan:** Formal analysis, Data curation.

Data Availability

The data sets and the R scripts required for reproducing the results presented in the paper have been uploaded in a Zenodo repository, at <https://doi.org/10.5281/zenodo.12732009> (<https://zenodo.org/records/12732009>).

Declaration of Interest

The authors have no competing interests to declare.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2024.10.028>.

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