Vocal convergence in the multi-level society of Guinea baboons

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ABSTRACT

The extent to which nonhuman primate vocalizations are amenable to modification through experience is relevant for understanding the substrate from which human speech evolved. One road to investigate the flexibility in vocal production has been to study differences in vocal behaviour between different social groups. We examined the vocal behaviour of Guinea baboons, *Papio papio*, ranging in the Niokolo Koba National Park in Senegal. Guinea baboons live in a multi-level society, with parties nested within gangs. We investigated whether the acoustic structure of grunts of 30 male baboons of five gangs differed in relation to social level and genetic relatedness. Males in this species are philopatric, resulting in increased male relatedness within gangs and parties. Grunts from members of the same gang were more similar to each other than across gangs (N = 435 dyads), but for parties within gangs we found no evidence for higher similarity (N = 169 dyads). Acoustic similarity did not correlate with genetic relatedness. Our study provides evidence for acoustic convergence in male Guinea baboon grunts; the observed nonlinear relationship between social level and acoustic similarity may reflect the limits of the extent to which vocal accommodation is possible, or even advantageous.

KEY WORDS: baboon, *Papio papio*, primate communication, relatedness, vocal learning

BACKGROUND

The structure of nonhuman primate vocalisations appears to be highly conserved [1]. Nevertheless, modifications in vocal output in relation to experience appear to be possible within species-specific constraints [2–4], which spurred debates about whether or not nonhuman primates show evidence for vocal learning [5,6]. To overcome the futile arguments about whether or not modification in vocal output should be taken as evidence for imitation, we recently proposed a framework that aims to distinguish between different

mechanisms that may contribute to acoustic variation as a result of auditory experience [7]; see also [8] for similar considerations about vocal learning more generally.

Of particular relevance in the present context are two of the mechanisms, namely 'specific auditory facilitation' and 'learning from success'. Specific auditory facilitation is based on the idea of a "common coding" framework, according to which perception and action are represented by the same system [9,10]. So, listening to specific calls may increase the likelihood of producing corresponding call variants by the listener. Variation in the exposure to specific variants should translate into corresponding variation in acoustic similarity. In other words, subjects that interact more frequently should be more similar to each other than those that interact less frequently. Acoustic similarity may also result from genetic relatedness, however. For instance, subjects that are highly related may also have a similar morphology of the vocal production apparatus [11]. Before conclusions about the role of experience can be drawn, it is therefore necessary to check whether potential acoustic variation between individuals can (also) be explained by genetic distance.

We here set out to test the idea of auditory facilitation by comparing the acoustic variation in male Guinea baboon, *Papio papio,* grunts. Guinea baboons are an intriguing model to examine the influence of auditory experience and social group membership, as they live in a nested multi-level society with male philopatry [12]. Males associate with specific females and young in 'units' [13]. Around four to five such units form 'parties', and 2-3 parties team up to form a 'gang' [14]. Males are spatially highly tolerant and show low levels of aggression [15]. They also form differentiated and stable relationships with other males [16]. During affiliative interactions with other group members, males produce low frequency tonal grunts (Fig. 1). Such grunts have been shown to increase the likelihood of a subsequent affiliative interaction or infant handling [17].

If specific auditory facilitation affects the structure of calls, subjects that interact frequently with one another should produce calls that are more similar to each other. In other words, members of the same party should have the greatest similarity, and members of the same gang should produce calls that are more similar to each other than to calls produced by members of another gang. If genetic relatedness affects vocal structure, dyads that are more highly related should reveal greater acoustic similarity.

METHODS

We obtained recordings of grunts from a total of 30 male baboons between 2010 and 2016. Thirteen of the males were members of the “Mare” gang and 14 of the “Simenti” gang, while 3 males resided in three different neighbouring gangs (“R”, “N”, and “O”). The Mare gang comprised two parties of 6 and 7 males each; the Simenti gang comprised two parties of 5 and 9 males each.

The vocalizations were recorded using Marantz PMD 661 recorders (D &M Professional, Longford, U.K.) with Sennheiser directional microphones (K6 power module + ME66 recording head; Sennheiser, Wedemark, Germany) equipped with Rycote windshields (RycoteWindjammer, Rycote Ltd., Stroud, U.K.). We used Avisoft SASLab Pro (Avisoft Bioacoustic, Berlin, Germany) to check the recording quality, and to label and extract grunts with sufficient quality and low background noise. We only used calls recorded at a maximum distance of 3 m.

We reduced the sampling frequency from 44.1 to 5 and 1 kHz to obtain an appropriate frequency resolution for the estimation of acoustic features, and calculated two 1024 pt Fast Fourier Transformation (FFT), one resulting in a frequency range of 2500 Hz (frequency resolution 5 Hz, temporal resolution 6.4ms) and a second FFT resulting in a frequency range of 500 Hz (frequency resolution of 1 Hz, and a temporal resolution of 16 ms). The resulting frequency time spectra were analyzed with a custom software program

LMA 2019, which allows a visual control of the accuracy of parameter estimation [18,19]. We focused on the following acoustic features: fundamental frequency (F0), peak frequency, distribution of frequency amplitudes and noisiness expressed as Wiener entropy (see Supplementary Material Table S1). In total, we included 780 grunts in the acoustic analysis. On average, we used 26 calls per subject in the analysis (range: 5-127). The Mare and Simenti gang males were represented by 390 and 366 grunts, respectively; the other three gangs by 7-10 grunts.

To quantify the acoustic similarity, we used a discriminant function analysis with which we obtained a pairwise F-value for the acoustic distance for each dyad. This approach has been applied in different studies examining relationships between acoustic structure and genetic or geographic distance [20–22]. To determine the F-values, we entered all 82 acoustic features into a stepwise discriminant function (DFA) with subject identity as grouping variable. The selection criterion for acoustic features to enter the discriminant function was $P_{in} = 0.05$ and to remove $P_{out} = 0.1$. The DFA used 33 acoustic features for the individual discrimination. F-values were calculated using IBM SPSS version 26.0 (IBM, Armonk, NY). To assess the classification result of the individual discrimination of male grunts, we performed a permuted DFA [23].

We extracted DNA from fecal samples using the First-DNA all tissue kit (Genial®). We characterized genetic variation by assessing the individual allele variation on 24 polymorphic autosomal microsatellite markers. The 24 markers were amplified using the Multiplex PCR Kit (QIAGEN) and fluorescent-labelled primers. PCR products were separated and detected through capillary gel electrophoresis on an ABI 3130xL Genetic Analyzer (Applied Biosystems®, USA). Microsatellite allele sizes were evaluated using Gene Mapper 5 (Applied Biosystems®). One locus (D1s548) showed signs of null alleles and significant deviations from Hardy-Weinberg equilibrium and was therefore excluded, resulting in a total of 23 loci included in the relatedness estimation (calculated with MICRO-CHECKER - version

2.2.3 [24] and the PopGenReport R package - version 3.0.0 [25], respectively). We used the R package “related version 1.0” [26,27] to estimate relatedness using R version 3.4.4 and RStudio version 1.1.456. The Queller-Goodnight estimator [28] showed the best performance and was thus chosen in the present analysis. This estimator ranges from -1 to 1. Negative values indicate that dyads are less related than on average, while positive values indicate that they are more highly related than on average (see [16] for a detailed description of the analysis).

These and the following statistical analyses were conducted in the R environment (version 3.6.2; [29]), using the RStudio interface (version 1.1.447; [30]). We used a mantel matrix correlation test (package “vegan” version 2.5.6) to test the correlation between acoustic and genetic variation. To test the effect of membership to a given social level, we applied categorical mantel tests, using “Same gang membership” (Yes/No) as the categorical predictor variable, and QG or F (transformed as ln(1+F)) as the continuous variable. This analysis was based on 435 dyads. To study the effect of party membership, we only considered dyads that belonged to the same gang (N = 169) and used a restricted permutation approach where males were permuted between parties within gangs. We used 1,000 permutations in all analyses, except the one for the variation between parties within gangs, where we used 10,000 permutations. The raw data and the code for statistical analysis are deposited at https://osf.io/h7q5r/?view_only=e24fb7b53e7a4c57a1fe67db5d2452ab

RESULTS

Confirming previous analyses, males were more highly related within gangs than between gangs (P = 0.009, N = 435), though the average (mean ± se) relatedness did not differ much within gangs (QG estimator: –0.003 ± 0.011, N = 169 dyads) and between gangs (–0.054 ± 0.014, N = 266 dyads). Within gangs, males in the same party were more highly related on

average (QG estimator: 0.024 ±0.024) than males that were not members of the same party (-0.029 ± 0.015, P = 0.035).

Grunts could be assigned to the correct individual significantly more frequently than by chance, with an average correct assignment of 38.1 % (chance level 3.3%, pDFA, P < 0.001). Across the five gangs, the acoustic similarity did not correlate with genetic similarity (r = -0.002, P = 0.497, Fig. S1). Yet, grunts of males within gangs were more similar to each other than between gangs (categorical Mantel test, P = 0.001). The variation in acoustic dissimilarity for within and between gangs is shown in Fig. 2A. Grunts of dyads in the same gang had a (mean ± se) dissimilarity of F = 1.08 ± 0.02, while grunts of dyads in different gangs had a mean dissimilarity of F = 1.25 ± 0.02. We found no evidence that grunts from males within parties were more similar to each other than between parties in the same gang (Fig. 2B, P = 0.6).

DISCUSSION

The structure of male grunts varied clearly between members of different gangs, but not between members of parties within a gang. Males in the same gang were also more highly related to one another, but this did not seem to account for the acoustic variation between gangs, as evidenced by the lack of correlation between genetic and acoustic similarity. Interaction frequency did not appear to account for the emergence of acoustic similarity either, as grunts of males in the same party were not acoustically more similar to each other than grunts of males in different parties in the same gang. This was somewhat surprising, given that in a previous study, dyads within parties were observed within 100 m proximity 65% of the instances, while dyads of different parties were found in 100 m proximity in 24% of the instances. Dyads of different gangs were observed within 100 m only 1 % of the time [14]. Moreover, grunts occur almost exclusively within members of the same party [17].

The absence of a high degree of similarity within parties discounts the idea of a linear relationship between auditory experience and vocal production. One possible explanation for the observed nonlinear relationship between social level and acoustic similarity may be that there are limits to the extent to which vocal accommodation is possible, or even advantageous. Indeed, there may also be selective pressure to maintain individual identity. Since the acoustic structure of grunts is relatively simple, this may additionally place a barrier on vocal convergence.

Alternatively, gang membership may have a special social value that promotes the adjustment of calls to that particular level. With the present data and in the absence of experimental manipulation, we are not able to distinguish between these two hypotheses, although the latter seems rather unlikely. Either way, it would be illuminating to track the vocal output of males that transfer between different levels, but since males are philopatric and dispersal is female-biased, such transfers are rare and rather unpredictable. We therefore have no data to test to which degree and over which time course males would adjust the structure of their calls.

The degree of variation in grunts between different social levels is relatively small though and it is not clear whether subjects pay attention to this variation. In a previous study [31], we tested male responses to the playbacks of grunts of males that share the same home range as the study males (“neighbours”) vs. to grunts of males living 50 km away (“strangers”). As control, we played back the grunts of males from the own gang. Surprisingly, males responded strongly only to the grunts from males of the own gang, but largely ignored neighbour or stranger males’ calls (see also [32]). In principle, these responses could be explained by recognition of the males’ individual characteristics. Yet, it might also be the case that males recognize the ‘sound’ of their own gang. Playbacks presenting artificially created grunts bearing the own gang’s characteristics vs. another gang’s characteristics would be needed to test this conjecture.

Taken together, we find evidence for a moderate degree of vocal convergence in Guinea baboons. The magnitude of the change is difficult to compare to those of other studies on nonhuman primates [3–5], given the differences in methodological approaches, but broadly appears to be in a similar range. Indeed, all these studies reported minor variation within the species-specific range. What does such group-specific variation tell us about the substrate for the evolution of speech? Perhaps not so much, as the observed variation could simply be a by-product of auditory experience, rather than volitional imitation, as in the case of human speech. We therefore iterate that simpler explanations for vocal plasticity need to be ruled out before we can safely claim to have identified precursors to human vocal learning [see 7].

CONCLUSION

While this study provides evidence for acoustic convergence in male Guinea baboon grunts, it also highlights that there are limits to the extent to which vocal accommodation is possible, or even advantageous. More generally, our findings add to the body of evidence that within species-specific constraints, subtle and (potentially) meaningful variation can be found in nonhuman primate vocalizations. This variation does not compare to the open-ended possibility of vocal imitation found in human speech, however.

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Author contributions

JF, KH and FW conceived the study, FW collected the data, FW and KH conducted the acoustic analyses, FDP and FT conducted the genetic analysis, JF and KH did the statistical analysis and prepared the figures, JF wrote the manuscript with input from all authors.

Figure Legends

Figure 1. Grunt examples from four different males. Frequency (kHz) on the y-axis, time (s) on the x-axis. The spectrogram was created using Avisoft-SASLab Pro 5.2 (1.024 pt FFT, sampling frequency: 11 kHz, time resolution: 2.9 ms, Flat Top window).

Figure 2. Acoustic variation between dyads that belong to (A) different gangs or the same gang, and (B) different parties or the same party within a gang. Boxplots with medians and interquartile range. Whiskers show values within 1.5 times of the inter-quartile range. Dots represent dyadic values.

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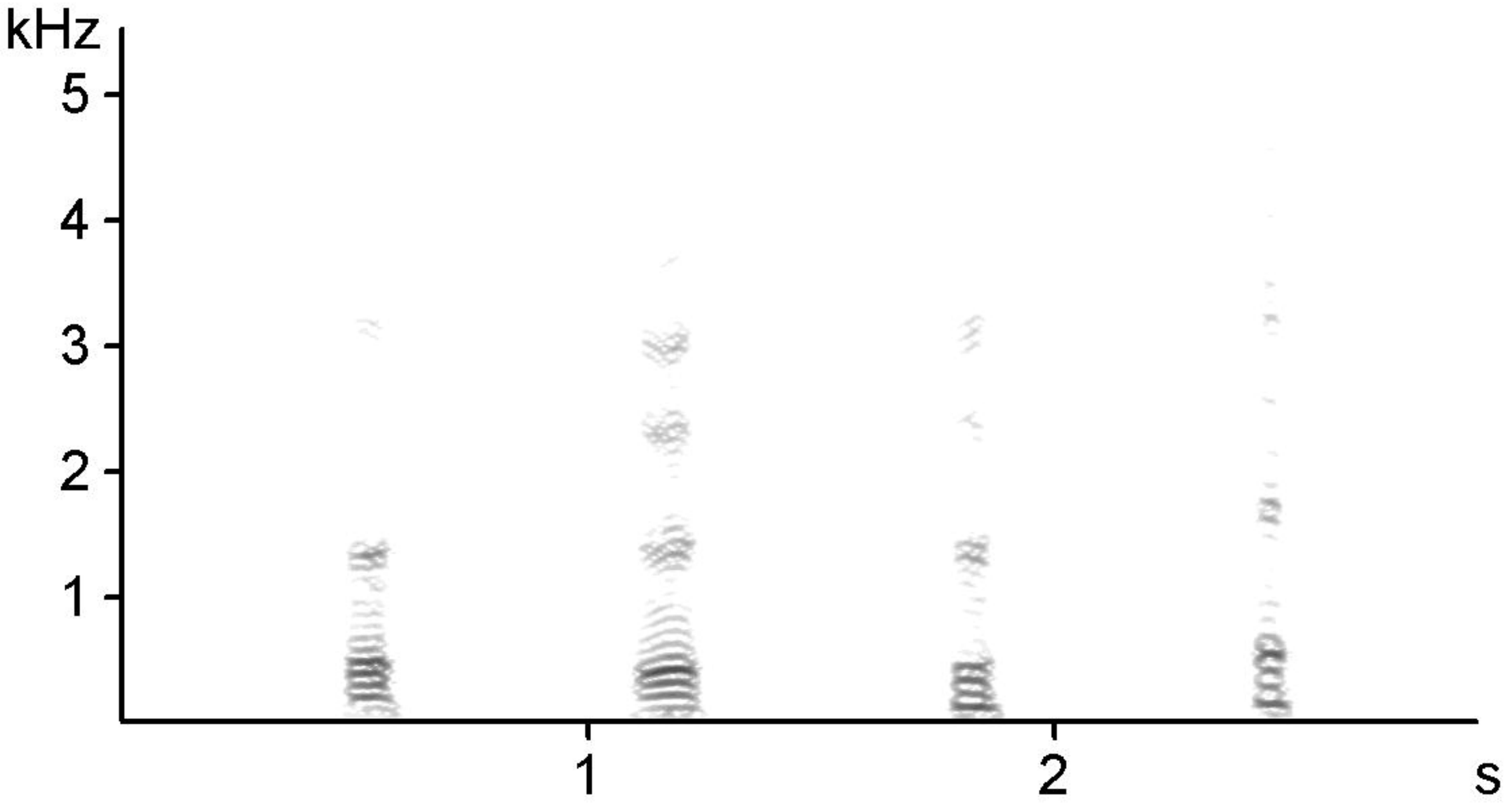
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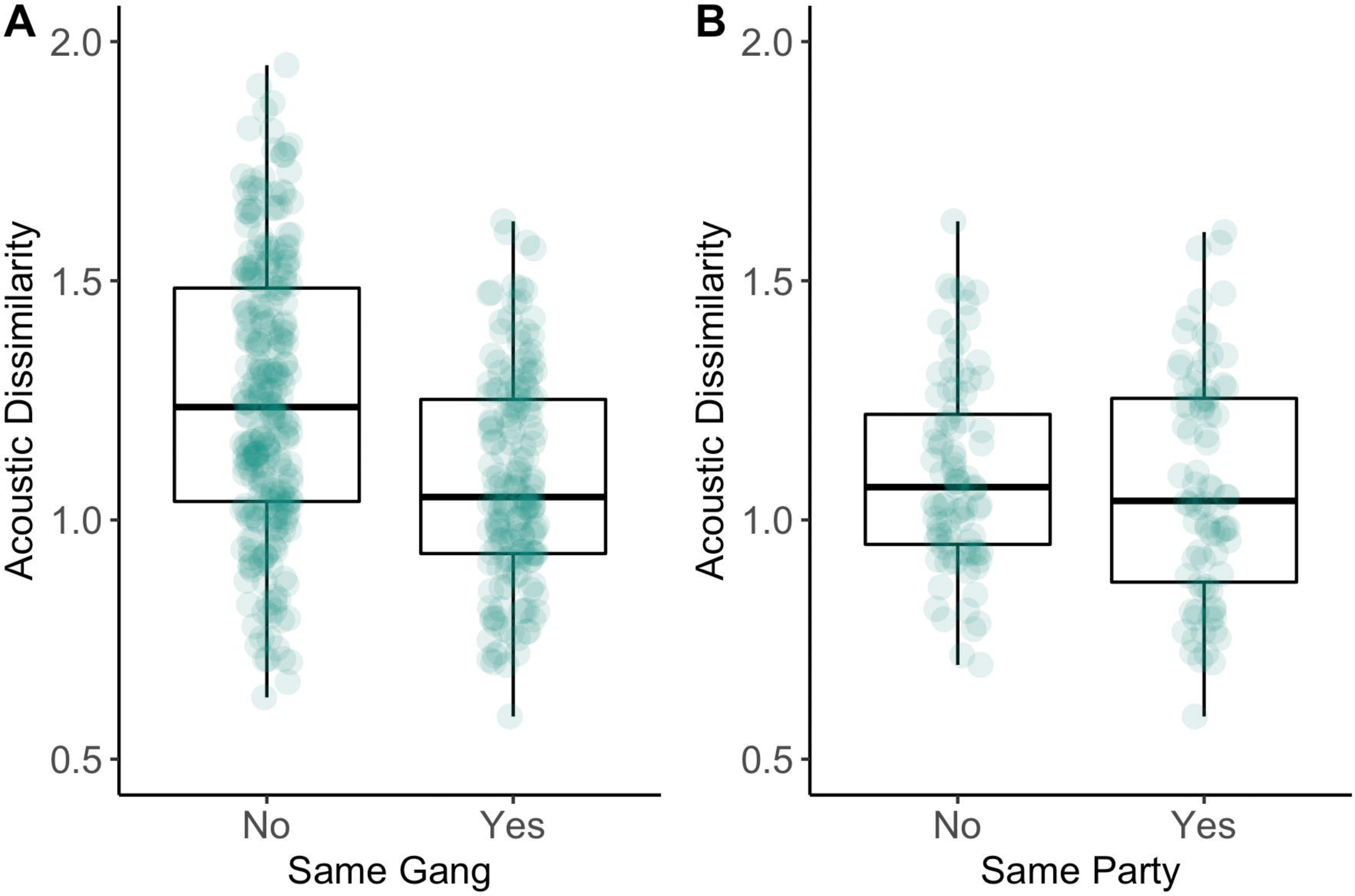
A
B
2.0
1.5
1.0
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Acoustic Dissimilarity
No
Yes
Same Gang
Same Party