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ORIGINAL RESEARCH

Goat kid recognition of their mothers' calls is not impacted by changes in fundamental frequency or formants

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Abstract

Features varying more between than within individuals are considered as potential cues for individual recognition. According to the source-filter theory of vocal production, the fundamental frequency of mammals' vocalizations depends on the characteristics of vocal folds, while Formants are determined by the characteristics of the vocal tract. Goat mothers and their kids (*Capra hircus*) display mutual recognition, and both source-related parameters (f0) and filter-related ones (Formants) have been shown to be individualized. Here, we aimed to identify if f0 and Formants are used by goat kids to recognize their mother's vocalizations. To do this, we independently modified these parameters in calls of goat mothers to different degrees (within or exceeding the range of natural intra-individual variability), and we played back these modified calls to their kids. We found no effect of f0 or Formants modification on the kids' reactions. Further analyses revealed that goat kids emitted fewer calls when modifications to f0 resulted in higher values of the first energy quartile, suggesting a role of the distribution of energy in the spectrum in maternal recognition. We propose that either: (i) f0 and Formants are not involved in goats' maternal recognition; (ii) goat kids have a tolerance for variation when recognizing their mother's calls that exceeds the performed shifts in these parameters; or (iii) goat kid maternal recognition is based on a combination of features and might be more flexible than previously thought, such that when one feature is modified, kids focus on other features. The effect of the spectral energy distribution modification on the kid responses, which depends both on f0 and Formant heights, suggests that (iii) is a likely explanation. Our findings support the hypothesis of complex individual acoustic recognition from the early stages of development in ungulates.

Introduction

Individual recognition is crucial for directed parental care (Briefer & McElligott, 2011a; Gokcekus et al., 2021; Searby & Jouventin, 2003), as well as for offspring survival (Padilla de la Torre et al., 2016) in social precocial mammals. In most group-living mammals, parent-offspring recognition develops quickly, usually in the few hours after birth, and is influenced by environmental constraints (Torriani et al., 2006). For example, the time of the first separation between mothers and new-born offspring influences the speed of development of recognition, as well as its directionality (Charrier et al., 2009). Mother-offspring

recognition at a distance mostly relies on visual and acoustic cues to infer the position of the young/parent, while recognition at close quarters is mostly sustained by olfaction (Torriani et al., 2006). In larger groups where risks of confusion are enhanced, accurate parent-offspring recognition prevents misdirected maternal care; particularly when the neonate depends entirely on its mother for food and/or when lactation requires a lot of energy (Linossier et al., 2021; Sèbe et al., 2010).

Vocalizations play an important role in individual recognition for social species since they can travel long distances and pass obstacles, allowing individuals to maintain contact (Yorzinski, 2017). To enable vocal recognition, features typically vary

more between than within individuals (Li et al., 2017), as can be assessed by the Potential Individual Coding (PIC). PIC values greater than 1 indicate a within-individual variation that is lower than the between-individual variation, and therefore that the feature is suitable for individual recognition. In species where contact calls have been shown to be individualized, offspring react more to the calls of their mothers compared to calls from other females. For example in ungulates, calves *(Bos taurus)* stay longer near and approach closer a loudspeaker broadcasting their mother's calls compared to one broadcasting another female's (Padilla de la Torre et al., 2016). Ungulate offspring use cues in both the frequency and temporal domains for maternal recognition (Sèbe et al., 2010, 2011).

In goats *(Capra hircus)*, mothers and kids have individualized contact calls (Briefer & McElligott, 2011a). Goats vocalizations are characterized by a clear harmonic structure, as well as strong frequency and amplitude modulations (Briefer et al., 2012). When isolated, goats produce two types of calls: contact calls and isolation calls, the latter characterized by higher pitch (Briefer & McElligott, 2011a; Siebert et al., 2011). Contact calls are produced either open or closed mouthed, with a close mouth altering the formant structure (Favaro et al., 2014). Sibling goat kids have more similar vocalizations compared to unrelated goat kids, and a study suggests that this effect might be independent of exposure to external sounds (Burke et al., 2020). However, goats also show some flexibility in their calls during development: the call of young kids living in the same group converge over time and become more similar than those raised in different groups (Briefer & McElligott, 2012).

Goat mother-offspring relationships are characterized by a specific, rapidly formed, and fairly stable maternal attachment (Hernández et al., 2012), leading to mutual recognition (Briefer & McElligott, 2011a). Mothers isolate before parturition and care exclusively for their own offspring, enhancing the mother-young bond and improving offspring survival by preventing separation (Briefer et al., 2012; Hernández et al., 2012). Mothers recognize their kid contact calls from 48 hours after birth, and this recognition lasts even after weaning and long-term separation (Briefer et al., 2012). Similarly, from at least 5 days old (i.e., also potentially younger), goat kids have been shown to differentiate between the calls of their mothers and other familiar females based on vocal cues (Briefer & McElligott, 2011a), although the precise features used in vocal recognition are not yet known. Later, from 2 to 5 weeks of age, goat kids depend mainly on milk, but tend to stay away from their mothers more than before, as at this age they start forming crèches with similarly aged kids (Lickliter, 1987; Miranda-de la Lama & Mattiello, 2010). Recognition of the mother's calls by their kids could be based on the fundamental frequency (f0; 'source', which depends on the characteristics of the vocal fold) and/or on the Formants ('filter', which are determined by the characteristics of the vocal tract; Taylor & Reby, 2010; Titze et al., 2015). Indeed, both f0 and Formants have previously been identified as potential markers of individuality in adult female bleats, with PIC values ranging from 1.31 to 3.33 for f0-related parameters, and 1.10–2.13 for parameters characterizing the second, third, and fourth Formants. Other alternative parameters could be the distribution of energy in the spectrum (i.e., how much energy each frequency has relative to others), as well as the extent of the amplitude and frequency modulations (Briefer & McElligott, 2011a).

Two types of paradigms can evaluate the cues used in vocal discrimination. First, investigating the extent to which vocal features are stable within individuals (i.e., characteristic) can be used to determine the likelihood that a certain feature will be involved in individual recognition (Pitcher et al., 2012; Sauvé et al., 2015). Second, playbacks can be carried out with modified calls in which features potentially used for individual recognition are altered one by one, while keeping the rest constant. These modified calls can then be played to the animals to assess whether these changes impair recognition (Charrier et al., 2003; Tamura et al., 2021). If recognition is impaired by the modification of a parameter, this suggests that it is used for recognition. Such experiments have shown, for example, that Australian sea lion *(Neophoca cinerea)* pups respond less to their mother's calls when f0 has been shifted (once, twice, or three times the standard deviation) than to natural calls, suggesting that they use this vocal feature for maternal recognition (Charrier et al., 2009).

The present study focused on determining if source-filter vocal parameters (e.g., f0 and Formant frequencies) are used by goat kids to recognize their mother's vocalizations. To this aim, we played back the vocalizations of mothers to their kids, where either f0 or Formants had been modified to different degrees (within or exceeding the range of natural intra-individual variability). We predicted that, if a feature is involved in vocal recognition, kids would react less to the modified vocalization than to the natural one, as the modification impairs recognition (Charlton, Huang, & Swaisgood, 2009; Charrier et al., 2009).

Materials and methods

Subjects and housing

Our subjects were 14 goat kids (six females and eight males), born from seven multiparous pygmy goat mothers and the same father in spring ($n = 10$) and summer 2011 ($n = 4$). All kids were born and raised at the WhitePost Farm (53°06′N, 1°03′W, UK). Kids' age ranged from 10 to 28 days (mean 17.08 ± 5.28 days) at the time of playbacks. The goats used in this study were kept indoors in a communal pen of 4.4 m × 4.5 m. Following the husbandry routine carried out by the farm employees, females who were about to give birth were isolated in a 2.5 m² pen within the communal pen and kept there with their kid(s) for 2–3 days. The aim was to allow adequate development of the mother–offspring relationship and prevent interference from other goats. Mothers and kids were then released in the communal pen.

Playback preparation

The mothers' calls were recorded 2–5 days before the playbacks, by separating kids from their mothers behind a fence (1–10 m) for no more than 5 minutes, two times a day, to elicit contact calls. Calls were recorded using a Sennheiser

MKH70 connected to a Marantz PMD660 recorder (sampling rate: 44.1 kHz) at 1–5 m from the mother. Frequencies are usually not affected by the distance at such short range (Towsey et al., 2012; Zeppelzauer et al., 2015) (see Briefer & McElligott, 2011b, 2012 for further details about the procedure). Open-mouth contact calls were then saved on a computer in wav, 16-bit, and visualized on spectrograms in Praat v.5.0.47 DSP Package (Boersma and Weenink, 2009) (window length = 0.01 s, dynamic range = 50 dB). Mothers were recorded over several sessions, and we extracted nonconsecutive good quality calls for preparing playback sequences. Calls used for the playbacks therefore originated from more than one session. In total, eight good-quality calls per individual (low level of background noise) were selected for preparing the five playback treatments.

We determined f0 and Formants resynthesis factors based on intra- and inter-individual variability of the mean f0 frequency value across the call ('f0Mean') and the mean frequency value of the fourth Formant ('F4Mean') from eight calls of 11 adult pygmy goats from Whitepost Farm (total 88 calls) recorded previously (Briefer & McElligott, 2011b). This sample of individuals included the seven mother goats whose calls were played back to kids in the current study. The fourth Formant was chosen for analyses due to its salience (high amplitude relative to lower formants), and also because it likely reflects vocal tract length and hence body size and identity of the emitter better than lower formants, which are more flexible and dependent on the vocal tract shape (Briefer & McElligott, 2011a; Charlton et al., 2017). The intra-individual variation (maximum – minimum value for each individual) was as follows (mean ± SD): f0Mean = 66.05 ± 36.52 Hz, F4Mean = 521.24 ± 262.17 Hz. The first modified call treatment was aimed to mimic a shift within the extreme range of within-individual variation, while the second treatment was aimed to mimic a shift outside this range. Resynthesis factors were created to account for the intra-individual variation for each mother goat. On average, the first shift was of about 70 Hz above the natural signal for f0Mean ('f0 Shift1') and about 520 Hz for F4Mean ('Formant Shift1'), and about twice these values for the second shift (140 Hz for f0Mean ('f0 Shift2') and 1040 Hz for F4Mean ('Formant Shift2')).

The preparation and modification of the playback sequences was carried out in Praat as follows: the eight selected calls were inserted in a sequence, interspaced by intervals of natural duration (0.98 s for adult goats: Briefer & McElligott, 2011b), made of the goat's usual background noise. The sequence was then repeated to obtain a 30s long sequence. To minimize pseudo-replication, sequences built for twin kids ($n = 7$ pairs) used the same mother calls but inserted in a different order, creating two different sequences. All calls in a given sequence were then rescaled to the same maximum amplitude. Following this sequence preparation, f0 and Formants were modified independently using a PSOLA-based algorithm with a custom Praat script (Pitcher et al., 2015), which shifted the f0 or Formant up by a predetermined resynthesis factor, supposedly leaving the other acoustic parameters (e.g., Formant and f0) unchanged (Appendix S3-S12). To define the resynthesis factor needed, the first call of each sequence was analysed to extract its f0Mean and F4Mean. Based on these extracted values, a resynthesis factor of 1.21–1.80 was used for f0 Shift1, and of 1.50–2.82 for f0 Shift2. For F4Mean, a resynthesis factor of 0.85–0.89 was used for Formant Shift1, and of 0.74–0.80 for Formant Shift2.

Modified calls of the mothers were examined to verify the modification and the absence of artefacts (Fig. 1). To verify that the quality of the speaker and the format (mp3) did not distort the calls, some calls were played through the speaker and re-recorded to visually assess their quality. In addition, the eight vocalizations constituting the sequence for each mother and in each treatment were then analysed using a script adapted from Reby and McComb (2003) and Charlton, Zhihe, and Snyder (2009) to obtain the precise f0 and Formants of all natural and modified calls played back. Since our f0 and Formant modifications could have also affected the distribution of energy in the spectrum, we additionally extracted the frequencies under which 25% ('Q25%'), 50% ('Q50%'), and 75% ('Q75%') of the energy can be found, to test the effect of these changes on the goat kid's responses. The following settings were used: Source-related vocal parameters (f0 mean, minimum, maximum values, and range) were measured by extracting the fundamental frequency contour of each call using a cross-correlation method ([Call: To Pitch (cc) command], f0: time step = 0.01 s, pitch floor = 70 Hz, pitch ceiling = 750 Hz). Filter-related (Formants) vocal parameters (F1, F2, F3, and F4 mean values and Formant dispersion) were measured by extracting the contour of the first four Formants of each call using Linear Predictive Coding analysis (LPC; [Call: To Formant (burg) command], time step = 0.01 s, maximum number of Formants = 4, maximum Formant = 5000 Hz (natural calls) to 6750 Hz (Formant Shift2), window length = 0.1 s). Finally, the energy quartiles Q25%, Q50%, and Q75% were measured on a linear amplitude spectrum applied to the whole call.

Experimental set up

The playback experiment was carried out in a 2.5 m^2 arena situated within the same barn but outside visual and hearing range from the kids' home pen. The testing arena was placed within a pen containing other species, to which the subjects were habituated to (i.e., sheep and llamas), surrounded on two sides by concrete walls, and on the two others by goat fences (Fig. 2). To prevent disturbance from other animals, one side was covered with a blanket. The loudspeaker and the camera were placed on the adjacent side, at about 2–4 m from the subject. The floor was covered with straw. Subjects were habituated to the pen for 5 minutes per day, alone, during 3–4 days before the first playback trial started.

Experimental procedure

Following Briefer and McElligott (2011b), after ensuring that it suckled from its mother before starting the procedure, each kid was placed with other pen mates (two to four kids together) for 1.5–2 h in the experimental set up before the first trial started, to trigger responses to maternal calls and allow the
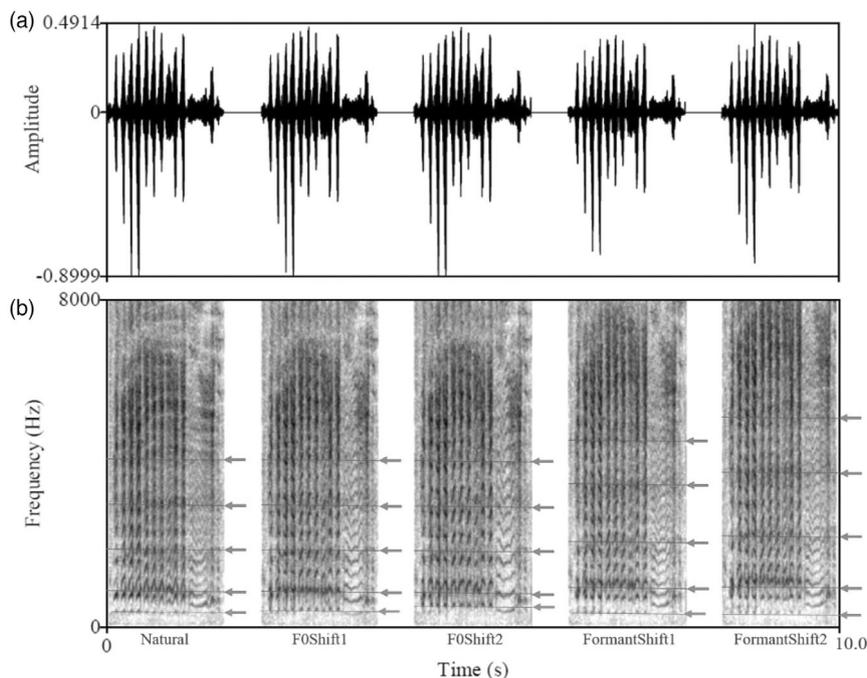
Figure 1 Example of a mother goat call oscillogram (a) and spectrogram (b) for each treatment. Arrows on the spectrograms indicate the Fundamental frequency f0 (lowest arrows) and the first four Formants (higher arrows).
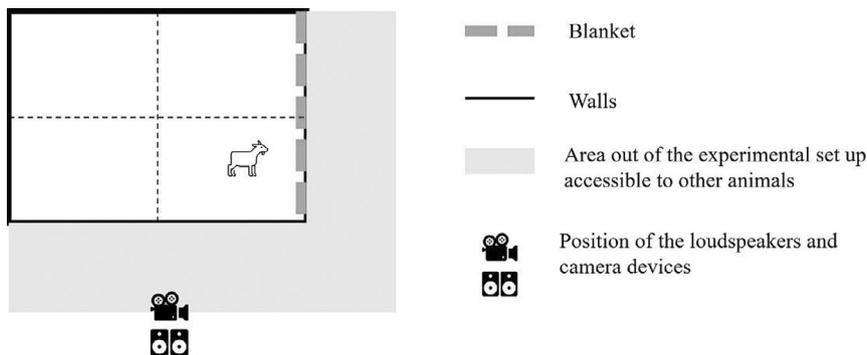

Figure 2 Schematic representation of the experimental set used during the playback sessions. Loudspeaker and camera devices were positioned about two meters away from the fences. A blanket was installed to reduce disturbance from surrounding animals that could pass by the experimental setup.

subjects to habituate to the pen. At the end of this habituation period, the other pen mates were removed, and the playback experiment started when subject was settled (i.e., returned to normal activities, exploring the pen without vocalizing). The call treatments, stored as high-quality mp3 files (sampling rate = 44.1 kHz; bit rate = 224 kbps), were played using a Skytronic TEC076 portable system (frequency response: 50 Hz–20 kHz ± 3 dB), at an intensity estimated to be normal for the goats (80 dB at 1 m; Briefer & McElligott, 2011b). Each kid was tested with the five playback treatments on 2–3 consecutive days (one to three treatments per day). To ensure relatively similar conditions and kid age between playbacks of f0 and Formant modifications, respectively, the order of testing

treatments was pseudo-randomized: the natural treatment could take place in any of the five trials, but f0 tests would take place on either the first, second, or third trial of testing whereas Formant tests would occur on either the third, fourth, or fifth trial. The behavioral response of the animals was recorded using a Sony DCR-SX50E camcorder. Kids were returned to their mother directly after each test.

Video analysis

The videos of the playbacks were scored while blind to the treatment. The behaviors were scored continuously, during the period preceding the playback ('Pre-playback'; duration:

40.93 s ± 6.06) and the rest of the video corresponding to the playback itself ('Playback'; duration: 37.27 s ± 4.37) using the software BORIS v7.9.8 (Friard & Gamba, 2016). The coded behaviors were divided in states, events and latencies. States behaviors were: looking towards the loudspeaker (evaluated with a 45° angle of head in direction to the device) and locomotion (with four legs moving). Event behaviors were: call (vocalizations of the goat kid). Latencies were recorded for the first call, to locomotion and to look towards the speaker after playback onset. Except for latencies, all behaviors were divided by the duration of the experimental phase for further analysis, resulting in 'ratios' for states (duration of the state/observation duration), and 'rates' for events (number of occurrence/observation duration).

To ensure reliability of the video coding, intra-observer reliability (Bateson & Martin, 2021) was calculated using the following procedure: 10 randomly selected videos were encoded twice in a random order. For each behavior, a correlation coefficient (r^2) was then calculated using a Pearson correlation test. For all behaviors, we obtained an $r^2 \geq 0.79$ (mean = 0.95; range = 0.79–0.99), suggesting good intra-observer reliability (Table S1).

Statistical analysis

Statistical analyses were conducted with RStudio (v1.3, R Core Team). Datasets are available (Perroux et al., 2022; Appendix S2). The effects of f0 and Formant manipulations were analysed separately. The dataset was hence split as follows: f0 treatments (natural, f0 shift1, and f0 Shift2) and Formant treatments (natural, Formant Shift1, and Formant Shift2). The same procedure (points 1–3 below) was applied to the two sub-datasets.

(1) For behaviors that could be measured before and after the playback onset (i.e., all except the latencies), a comparison was made between these two periods to select behaviors that could be considered as a reaction to the calls (i.e., that were affected by the auditory stimuli). To this aim, a Linear Mixed-Effect Model (LMM) was run for each behavioral response, including the behavioral response as the outcome variable, the period (before or after playback) as a fixed factor, and the identity of the subject nested within the identity of its mother as a random factor. Behaviors that differed significantly between the two scoring periods were selected for further analyses.

(2) To test for the effect of the playback treatment on the responses of the kids, for each extracted acoustic parameter, the mean acoustic values of the calls of each mother in each treatment were subtracted to the mean value of the natural treatment, to obtain the actual shift (i.e., the natural vocalization was therefore fixed at zero, and each value given refers to that difference, hereafter 'playback shift'). One LMM model was built for each selected behavior, entered as an outcome variable, and for each acoustic parameter measured (f0: mean ('Mean f0'), minimum ('Min f0'), maximum ('Max f0') values and range ('Range f0'); and Formants: (Mean F1, F2, F3 and F4 values and

Formant dispersion), playback shift values were entered as a continuous fixed factor. The effect of the modifications to the spectral energy distribution (Q25%, Q50%, and Q75%) were tested in the same way (by including the playback shift values as fixed factors), in both f0 and Formant datasets separately. In all models, the identity of the subject nested within the identity of its mother was used as a random effect to control for repeated measurements of the same subjects and potential similarities between twins.

(3) We then investigated the impact of modifying f0 on Formants, and vice versa, to validate our PSOLA-algorithm procedure. To this aim, we ran further LMMs including the mean value, for each playback sequence of each mother's calls, of the vocal parameters extracted from the acoustic analyses of the calls played back as an outcome variable (in separate models, f0 values: Mean f0, Min f0, Max f0, and Range f0; and Formants values: Mean F1, F2, F3, and F4 values and Formant dispersion). Each model included the playback treatment as a fixed effect (i.e., Natural, Formant Shift1, and Formant Shift2 for LMM carried out on f0 values and Natural, f0 Shift1, and f0 Shift2 for LMM carried out on Formant values), and the identity of the mother as a random factor. For models where the treatment influenced the acoustic features, post-hoc Tukey tests were conducted. The results of these models can be found in Appendix S1 (Tables S3 and S4). Similar tests were conducted for spectral energy distribution values (Q25%, Q50%, and Q75%).

For all LMMs, we checked the residuals of the models graphically for normal distribution and homoscedasticity (simulateResiduals function, package DHARMa, Hartig, 2022). If the assumptions were not met, a logarithmic transformation was used. When the assumptions of normality and homoscedasticity were not met despite a logarithmic transformation, the data were transformed to binary data (superior to the median in the treatment = 1, inferior to the median = 0) and input into Generalized Linear Mixed-Effect Models (GLMM) instead with the same fixed, control, and random factors as the LMM models (function glmer, package lme4; Bates et al., 2015). Precise model types can be found in the Appendix S1: Table S5. *P*-values were calculated by comparing models with and models without the term of interest using parametric bootstrap methods (1000 bootstrap samples; PBmodcomp function, package pbkrtest, Halekoh & Højsgaard, 2014). To this aim, models were fitted with maximum likelihood.

One of the mothers died due to causes unrelated to the experiment during the testing period (between playback sessions). To ensure that the responses of her twin offspring did not differ from those of other kids, Wilcoxon signed rank exact tests were used to compare the mean values of each behavior in each treatment including the responses from these two kids with the variance when the response of these kids after their mother's death were excluded (three trials for one kid and four trials for the other kid). Since these differences were not significant (f0: $V = 39$, *P*-value = 0.144; Formants: $V = 88$, *P*-value = 0.546), the responses of these two kids were included in analyses.

Ethical note

Animal care and all experimental procedures were in accordance with the Guidelines for the treatment of animals in behavioral research and teaching (2006). The experiments were carried out in 2011. At that time, no ethical approval was required at the host university for non-invasive playback experiments.

Results

Behaviors affected by the playback

For both f0 and Formant treatments, the following goat kid behaviors significantly differed between before and after the playback onset: call rate (LMM: f0, $P < 0.0001$; Formants, $P < 0.0001$), locomotion ratio (LMM: f0, $P < 0.05$; Formants, $P < 0.05$) and looking ratio (LMM: f0, $P < 0.01$; Formants, $P < 0.01$; Appendix S1: Table S2). These behaviors and the corresponding latencies were selected for further analysis.

Effect of f0 modifications on maternal recognition

f0 modifications did not affect kid responses to the playbacks (Table 1; e.g., Fig. 3). The order in which goat kids underwent the treatments had a significant effect on nine models for behaviors coded as rates and ratios (call, locomotion and looking towards the speaker) out of 12 and did not impact the models for latencies (Appendix S1: Table S6, Figure S1). Goat kid's behavior before playback onset affected their behavior after the onset on all models for all behaviors coded as rates and ratios (Appendix S1: Table S7).

Effect of formants modifications on maternal recognition

Formant modifications did not affect kid responses to the playbacks (Table 2; e.g., Fig. 4). The order in which kids underwent the treatments had a significant effect on all models for locomotion and looking towards the loudspeaker latencies, and for call rate and locomotion ratio (Appendix S1: Table S8, Figure S2). Goat kid's behavior before playback onset affected their behavior after the onset on all models for call rate and locomotion ratio (Appendix S1: Table S9).

Effect of spectral energy distribution on maternal recognition

Within the Formant treatments, spectral energy distribution differed between all three treatments (LMM: Q25%, $P < 0.001$; Q50%, $P < 0.001$, Q75%, $P < 0.001$; Tukey's HSD test: $P < 0.001$). However, these modifications to the spectral energy distribution did not affect kid responses to the playbacks (Appendix S1: Table S10).

In f0 treatments, only Q25% and Q50%, but not Q75%, differed between the treatments (LMM: Q25%, $P < 0.001$; Q50%, $P < 0.001$, Q75%, $P > 0.05$). Further two-by-two comparisons showed that these modified sequences differed in their energy quartiles from natural ones, but not between each other (Tukey's HSD test: Natural to f0 Shift1: $P < 0.001$; Natural to f0 Shift 2: $P < 0.0001$; f0 Shift1 to f0 Shift2: $P > 0.05$, Appendix S1: Table S11). The rate of calls emitted by kids decreased with the shift in Q25% towards higher values (LMM: $P < 0.01$, Fig. 5).

Discussion

Mother goats and their kids display mutual recognition, and kids recognize their mother based on vocal cues from at least 5 days old (Briefer & McElligott, 2011a). However, the vocal parameters used for achieving this vocal recognition remain unknown. We investigated whether goat kids would react to modified versions of their mother's calls, using two types of changes (to fundamental frequency (f0) and Formants) and two intensities of modifications (within the intra-individual variability or exceeding this variability). We found that call rate, locomotion ratio, and looking ratio were affected by the playback onset. However, goat kids responded as much when exposed to natural maternal vocalizations, compared to when the f0 or the Formants were modified. However, further analyses testing how changes in the spectral energy distribution due to our f0 and Formant modifications affected the kid responses revealed that their call rate decreased with upward shifts in the frequency value at the upper limit of the first quartile of energy (Q25%). We suggest that goat kids recognize their mother vocalizations based on several possible non-exclusive mechanisms: (i) f0 and Formants are not involved in maternal recognition in goats (Carlson et al., 2020); (ii) goat kid maternal recognition sensitivity exceeds the shifts we performed (Aubin & Jouventin, 2002); or (iii) goat kid maternal recognition

Table 1 Effect of actual shifts in f0 among playbacks of natural calls (no shift), f0 Shift1 (i.e., within the natural variability), and f0 Shift2 (i.e., exceeding the natural variability of the mother's vocalization) on goat kids' behaviors

P-values	Latency call	Latency locomotion	Latency look	Call rate	Locomotion ratio	Looking ratio
Max f0	0.652	0.377	0.366	0.649	0.289	0.646
Mean f0	0.519	0.293	0.247	0.377	**0.159**	0.433
Min f0	0.484	0.515	0.236	0.482	**0.156**	0.291
Range f0	0.851	0.624	0.989	0.738	0.766	0.442

f0 values were obtained by subtracting each mean frequency value of the playback sequence to the mean values of the natural playback of the corresponding individual, giving a value of zero for the natural call. Linear Mixed-Effect Models (LMMs; P-values extracted using parametric bootstrap) did not reveal any significant effect of the shifts on goat kids' behavior. In bold are the lowest P-values, whose relationships are illustrated in Fig. 3.
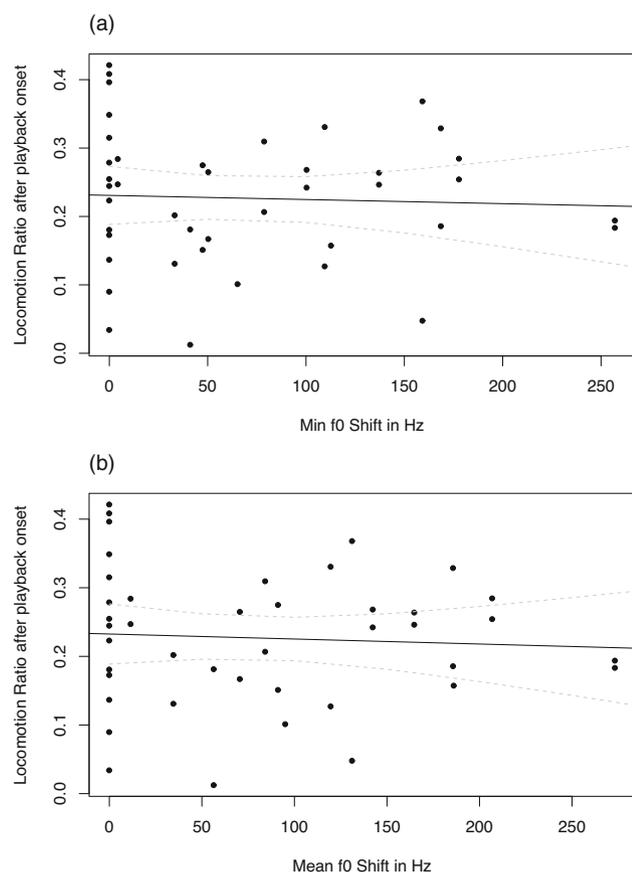
Figure 3 Effect of the actual shift in minimum (a) and mean (b) f0 on locomotion ratio (time spent performing the behavior divided by the total duration of the video sequence) after playback onset over the three treatments: natural voice of the mother (set at 0 Hz), a positive shift within the natural range (about 70 Hz above natural f0 Mean), and a positive shift exceeding the natural range (about 160 Hz above natural f0 Mean). Dots represent the data, and the black line represents the predicted effect given by the LMM model. In grey are given the 95% predicted confidence intervals.

is based on several features and might be more flexible than previously thought, such that when one main feature is modified, kids focus on other features (Charrier et al., 2003).

Fundamental frequency and formants in maternal recognition

We had predicted that f0 could be a cue used for individual recognition, because its contour in mother contact calls shows a high Potential for Individual Coding (PIC; start, mean and maximum f0; Briefer & McElligott, 2011b). Similarly, second, third, and fourth Formants' minimum, mean, and maximum values have PIC values >1 in goat mother calls (Briefer & McElligott, 2011b), making them suitable as well for individual recognition. Because we did not find any effect of f0 or Formants modification on maternal recognition, our findings are in line with previous observations suggesting that producing individualized vocalizations does not always result in individual recognition (Carlson et al., 2020). Indeed, sometimes, receivers use less individualized features to identify the sender. In pandas (*Ailuropoda melanoleuca*), mean f0 is highly individualized but females use amplitude modulations to recognize male conspecifics (Charlton, Huang, & Swaisgood, 2009). Our results suggest that goat kids might not use f0 and the Formants for individual recognition of their mothers, despite these parameters being highly individualized.

We expected that kids would react less to modified than natural vocalization of their mothers. It is more adaptive for goat kids to only reply to the vocalization of their mothers so that they do not reveal their location to potential predators (Briefer & McElligott, 2011a; Padilla de la Torre et al., 2016). In Australian sea lions, pups look and approach the speaker less when f0 of their mothers' vocalizations have been changed (of once, twice, or three times the standard deviation) than when hearing their mothers' natural vocalizations (Charrier et al., 2009). By contrast, fur seal pups have a high tolerance to variation in vocal parameters (Charrier et al., 2003) In our study, goat kids did not differentiate between natural and modified calls of their mothers even when the intra-individual variation was exceeded. This might suggest that goat kids are tolerant to variation in parameters, at least those studied here (f0 and Formants). However, we only tested kids between 10 and 28 days old. We thus cannot rule out that younger (or older) kids might have responded differently to f0 and Formant modifications, as their stage of development may impact their motivation and hence responses (Miranda-de la Lama & Mattiello, 2010). Further research could thus investigate age-dependant factors in maternal recognition.

Table 2 Effect of actual shifts in Formants among playbacks of natural calls (no shift), Formant Shift1 (i.e., within the natural variability), and Formant Shift2 (i.e., exceeding the natural variability of the mother's vocalization) on goat kids' behaviors

P-values	Latency call	Latency locomotion	Latency look	Call rate	Locomotion ratio	Looking ratio
Mean F1	0.306	0.506	0.43	0.934	0.402	0.69
Mean F2	0.400	0.453	0.715	0.924	0.470	0.727
Mean F3	0.406	0.573	0.526	0.923	0.450	0.796
Mean F4	0.826	0.566	0.909	0.757	**0.125**	0.364
Dispersion	0.545	**0.156**	0.744	0.687	**0.128**	0.336

Formant values were obtained by subtracting each mean frequency value of the playback sequence to the mean values of the natural playback of the corresponding individual, giving a value of zero for the natural call. Linear Mixed-Effect Models (LMMs; P-values extracted using parametric bootstrap) found no significant effect of the shifts on goat kids' behavior. In bold are the lowest P-values, whose relationships are shown in Fig. 4.
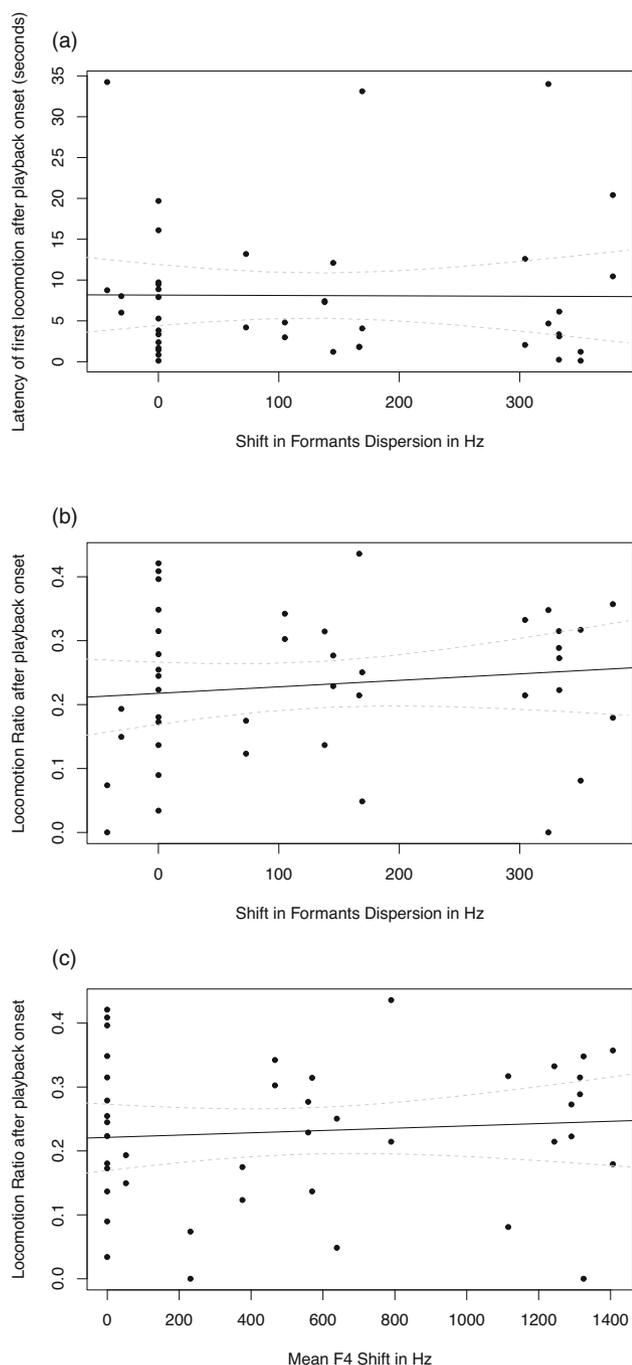
(a)

(b)

(c)

Figure 4 Effect of the actual shift in Formant dispersion on the latency of the first locomotion (a) and locomotion ratio (b), and of the shift in mean value of F4 on locomotion ratio (c) after playback onset over the three treatments: natural voice of the mother (set at 0 Hz), a positive shift within the natural range (about 520 Hz above natural F4 Mean), and a positive shift exceeding the natural range (about 1040 Hz above natural F4 Mean). Ratios were obtained by dividing the duration of the behavior by the total duration of the video sequence. Dots represent the data, and the black line represents the predicted effect given by the LMM model. In grey are given the 95% predicted confidence intervals.
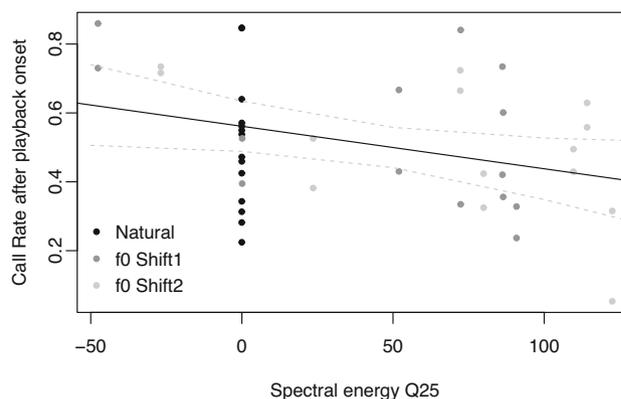
Figure 5 Effect of the actual shift in the frequency under which 25% of the energy in contained (Q25%) on the rate of contact calls emitted by the goat kid after playback onset over the three treatments: natural contact call of the mother (black dots), a positive shift within the natural range of f0 (dark grey dots), and a positive shift exceeding the natural range of f0 (light grey dots). Rates were obtained by dividing the number of events by the total duration of the video sequence. Dots represent the data, and the black line represents the predicted effect given by the LMM model. In grey are given the 95% predicted confidence intervals.

Goat maternal recognition may alternatively rely on duration, amplitude modulation, or frequency modulation, which also differ between individuals, although to a lesser extent than f0 and Formants parameters (Briefer & McElligott, 2011a). In lambs, suppressing amplitude modulation while keeping the natural frequency modulation was found to prevent lambs from identifying their mother's voice (Sèbe et al., 2011). In fur seals, pups can recognize their mother calls despite a suppression of the amplitude modulation, but their recognition ability is impaired by a reversed temporal frequency pattern (Charrier et al., 2003). In the same study, fur seal pups could recognize their mother's call based on the first 25% of the call, but the recognition was impaired if only 10 or 20% of the call was broadcasted, and there was no recognition with only the last 25% of the call (Charrier et al., 2003). In goats, spectral energy distribution (i.e., the distribution of the energy of the signal in the frequency domain) was also found to be individualized (Briefer & McElligott, 2011a). Our additional analyses on related parameters suggest that the frequency value at the upper limit of the first energy quartile (Q25%) may play a role in maternal recognition, as changes to this parameter induced by our f0 modifications led to decreased calling responses from goat kids. However, further tests should be carried out, in which the spectral energy distribution is modified further and in a more consistent way than in our study, as well as with a larger sample size.

Effect of the PSOLA-based algorithm on the acoustic pattern of goat mothers vocalizations

Despite f0 and Formants being theoretically independent of each other (Charlton et al., 2017; Taylor & Reby, 2010),

modifying Formants using a PSOLA-based algorithm had an impact on the mean, maximum, and minimum value of the fundamental frequency, while a modification of fundamental frequency impacted the first, third, and fourth Formants as well as Formants dispersion. These results imply that, when measuring the behavioral response to targeted modified factors, there is a possibility that subjects' behavior reflected unwanted modifications of other factors. However, even in natural goat vocalizations, f0 and Formants values are correlated to some extent (Briefer & McElligott, 2011a, Appendix S1: Table S11). The fundamental nature of the algorithm we used could explain these unwanted effects. PSOLA-based algorithm for frequential modifications rely on precision pitch marks (Rudresh et al., 2018). It has been found to be of insufficient quality for large f0 changes, and particularly very high f0 alterations, by creating imperfections and serious errors (Owsianny, 2019). Considering how goat f0 is naturally quite variable and high, and was positively shifted in the present experiment, the PSOLA-based algorithm may have produced stimuli where the overall call pattern was not preserved.

Conclusion

To conclude, even though they are individualized (Briefer & McElligott, 2011a), we did not find evidence to suggest that f0 and Formant features of the mother's voice are used for maternal recognition in goats. Instead, it seems that the distribution of the energy in the lower part of the spectrum might be used, but additional tests should be carried out to examine that suggestion. Overall, it is likely that goat kid recognition of mother calls is facilitated by either different acoustic parameters than f0 or Formants, or by complex relationships between a suite of parameters, rather than individual ones. Thus, our findings are in line with the hypothesis that individual acoustic recognition of mother calls by ungulate offspring can be complex (not based on single features) and might be flexible.

Acknowledgments

Author contributions

EFB and AGM conceived the ideas and designed methodology; EFB collected the data; TAP and EFB analysed the data; TAP led the writing of the manuscript. All authors contributed critically to the writing of the manuscript and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary Tables S1 to S11 and supplementary figures S1 and S2.

Table S1. Intra-observer reliability for video coding in BORIS Software. 10 videos were randomly selected and coded twice, before comparing each behavior encoded in both videos using Excel function r^2. All behaviors had a good intra-observer reliability (min: 0.793; max: 0.992).

Table S2. P-values, R²m and R²c obtained by comparing LMM models including the period (i.e., before vs after playback onset) to models not including period (null models) for each of the behavior measured during the video analysis. Behaviors in bold were found to significantly differ and were selected for further analysis.

Table S3. Effect of f0 treatments on Formant values in mother goat calls: natural calls, f0 Shift1 (i.e., f0 positively shifted by one time the standard deviation of the caller), and f0 Shift2 (i.e., f0 positively shifted by twice the natural standard deviation of the caller). The results of Tukey's HSD test for each measure in which the model was significantly influenced by the treatment treatment are listed (i.e., four out of five measures). Significant terms' P-values are given in bold.

Table S4. Effect of f0 treatments on Formants values in mother goat calls: natural call, Formant Shift1 (i.e., Formants positively shifted by one time the standard deviation of the caller), and Formant Shift2 (i.e., Formants positively shifted by twice the natural standard deviation of the caller). The results of Tukey's HSD test for each measure in which the model was significantly influenced by the treatment are listed (i.e., three out of four measures). Significant terms' P-values are given in bold.

Table S5. Different model types used throughout the statistical analysis.

Table S6. Effect of the order of the treatments on the behavioral response of goat kids to modified playback of their mothers in models addressing the f0 acoustic parameters. Hereafter are given the P-values of this effect for each LMM model. Results were obtained using "drop1" function in the package "stats" on R software. Significant results appear in bold.

Table S7. Effect of the behavior before the treatments on the behavioral response of goat kids to modified playback of their mothers in models addressing the f0 acoustic parameters. Hereafter are given the P-values of this effect for each LMM model. Results were obtained using "drop1" function in the package "stats" on R software. Significant results appear in bold.

Table S8. Effect of the order of the treatments on the behavioral response of goat kids to modified playback of their mothers in models addressing the Formant acoustic parameters. Hereafter are given the P-values of this effect for each LMM model. Results were obtained using "drop1" function in the package "stats" on R software. Significant results appear in bold.

Table S9. Effect of the behavior before the treatments on the behavioral response of goat kids to modified playback of their mothers in models addressing the Formant acoustic parameters. Hereafter are given the P-values of this effect for each LMM model. Results were obtained using "drop1" function in the package "stats" on R software. Significant results appear in bold.

Table S10. Effect of PSOLA-based algorithm modification of Formant values on spectral energy distribution in mother goat calls in three treatments: the natural call, the Formant Shift1 (i.e., Formants positively shifted by one time the standard deviation of the caller), and Formant Shift2 (i.e., Formants positively shifted by twice the natural standard deviation of the caller). The results of Tukey's HSD test for each measure in which the model was significantly influenced by the treatment treatment are listed. Significant terms' P-values are given in bold.

Table S11. Effect of PSOLA-based algorithm modification of f0 values on spectral energy distribution in mother goat calls in three treatments: natural calls, f0 Shift1 (i.e., f0 positively shifted by one time the standard deviation of the caller), and f0 Shift2 (i.e., f0 shifted by twice the natural standard deviation of the caller). The results of Tukey's HSD test for each measure in which the model was significantly influenced by the treatment treatment are listed (i.e., four out of five measures). Significant terms' P-values are given in bold.

Figure S1. Effect of the order of the treatment (1–5) on locomotion ratio (A), looking rate (B) and call rate (C) of goat kids exposed to the playbacks of their mother's vocalisations (over three treatments: natural voice of the mother (no shift), a positive shift of f0 within the natural range, and a positive shift of f0 exceeding the natural range).

Figure S2. Effect of order of the treatment (1–5) on latency of the first movement (A), the latency of the first look at the loudspeaker (B), locomotion ratio (C) and call rate (D) of goat kids exposed to the playbacks of their mother's vocalisations (over three treatments: natural voice of the mother (no shift), a positive shift of Formants within the natural range, and a positive shift of Formants exceeding the natural range).

Appendix S2. R Scripts used for statistical analysis.

Appendix S3-S4. Goat mother call used in the playback sequence of the f0 Shift1 treatment.

Appendix S5-S6. Goat mother call used in the playback sequence of the f0 Shift2 treatment.

Appendix S7-S8. Goat mother call used in the playback sequence of the Formant Shift1 treatment.

Appendix S9-S10. Goat mother call used in the playback sequence of the Formant Shift2 treatment.

Appendix S11-S12. Goat mother call used in the playback sequence of the natural treatment.