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Nonlinear vocal phenomena affect human perceptions of distress, size and dominance in puppy whines

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Abstract

While nonlinear phenomena are widely reported in animal vocalisations, often causing perceptual harshness and roughness, their communicative function remains debated. Several hypotheses have been put forward: attention grabbing, communication of distress, exaggeration of body size and dominance. Here, we use state-of-the-art sound synthesis to investigate how NLP affect the perception of puppy whines by human listeners. Listeners assessed the distress, size, or dominance conveyed by synthetic puppy whines with manipulated NLP, including frequency jumps, and varying proportions of subharmonics, sidebands, and deterministic chaos. We found that the presence of chaos increased the puppy’s perceived level of distress and that this effect held across a range of representative f_o levels. Adding sidebands and subharmonics also increased perceived distress among listeners with extensive caregiving experience with pre-weaned puppies (e.g., breeders, veterinarians). Finally, we found that whines with added chaos, subharmonics, or sidebands were associated with larger and more dominant puppies, although these biases were attenuated in experienced caregivers. Together our results show that nonlinear phenomena in puppy whines can convey rich information to human listeners and may thus be crucial for offspring survival during breeding of a domesticated species.

Keywords

Nonlinear vocal phenomena, puppy whines, human perception, interspecific communication, animal communication

Introduction

There is now widespread evidence that vertebrate vocal signals communicate both static information (e.g., relatively stable physical and social attributes) and dynamic information (e.g., transient emotional and motivational states) about the animals that produce them [1,2]. Investigating how these signals are emitted, and how mechanisms of vocal production determine their acoustic structure, has enabled researchers to better understand their evolution and functions [2].

In mammals, the production of vocalisations is initiated in the larynx by vocal fold vibration [3]. The rate at which the vocal folds vibrate determines a key feature of vocal signals, their fundamental frequency (f_o), which is largely responsible for their perceived pitch [3]. While vocal fold vibration is typically regular, perturbations can occur, causing abrupt changes in the tonal structure of acoustic signals [4,5]. This results in acoustic irregularities known as nonlinear phenomena (hereafter NLP), which are widely reported in the vocalisations of terrestrial mammals (e.g., koalas (*Phascolarctos cinereus*): [6]; marmots (*Marmota marmota*): [7]; chimpanzees (*Pan troglodytes*): [8]; meerkats (*Suricata suricatta*): [9]; giant pandas (*Ailuropoda melanoleuca*): [10]; dogs (*Canis lupus familiaris*): [11,12]; North American elk (*Cervus canadensis*): [13]; cows (*Bos taurus*): [14] African elephants (*Loxodonta*

Africana): [15]), including humans (*Homo sapiens*) [16,17]. Generally, the presence of NLP in vocalisations is responsible for perceived harshness, roughness and instability [18].

Four main types of NLP in animal vocalisations are frequency jumps, subharmonics, sidebands, and deterministic chaos. *Frequency jumps* correspond to sudden changes in vocal fold vibration [19]. *Subharmonics* can appear when one vocal fold vibrates at a period corresponding to an integer fractional value of the second vocal fold (e.g., 1:2, 2:3) [20], while *sidebands* (resulting from biphonation) are produced by the vibration of two independent sound sources (e.g., vocal folds vibrating at two independent frequencies) [4]. Finally, *deterministic chaos* (hereafter chaos) usually occurs when vocal folds vibrate in asynchronous nonperiodic regimes [5]. Because of their ubiquity in mammal calls, a consensus is emerging that NLP are not merely by-products of vocal production but rather function to communicate information about the caller [4,5]. However, it remains unclear what kind of information NLP transmit.

It has been suggested that NLP are vocal indicators of high arousal [7,11,15,21] in contexts associated with distress (e.g., during separation from conspecifics or immediate risk of predation) [22]. Specifically, chaos represents the most severe and perceptually harsh form of vocal nonlinearity [18] characterizing the distress vocalisations of several mammal species [10,11,15,21–23], including humans [16,17]. For instance, perceptions of distress increase with the presence of NLP in nonverbal vocalisations of human infants [16] and adults [17]. This has led to the suggestion that a possible biological function of NLP may be to reduce habituation in receivers by making these calls unpredictable and thus difficult to ignore [9,24–26].

Aside from NLP, f_0 (perceived as pitch) and formant frequencies (vocal tract resonances that influence perceived timbre) also affect the perceptual quality of vocalisations. In many terrestrial mammals, formants reliably predict inter-individual differences in body size, whereas f_0 is usually a better predictor of dominance status [27]. Indeed, animals in aggressive motivational states commonly produce harsh low-pitched calls [28] to potentially signal and/or exaggerate their size and dominance [2]. These signals can therefore play a key role in determining the outcome of agonistic interactions, for instance during sexual competition or territorial defence [27]. In this context, another hypothesis regarding the potential functions of NLP may be to exaggerate perceived size and dominance [4,5]. Some NLP can indeed lower perceived pitch, enhancing the perceptibility of vocal tract resonances by increasing spectral density, and potentially, may affect perceptions of the vocaliser's size and dominance [4,18]. Together, several hypotheses have thus been put forward regarding the functions of NLP: attention grabbing, communication of distress, and/or size or dominance exaggeration.

Previous investigations of the perceptual effects of NLP in nonhuman animal vocalisations have focused on a single type (e.g., chaos in lizards (*Liolaemus chiliensis*): [29]; chaos in marmots: [24]; subharmonics in meerkats: [9]; chaos in red deer (*Cervus elaphus*): [26]). Past studies also typically relied on NLP variation in natural vocal sounds (frogs (*Odoranna tormota)*: [30]; meerkats: [9,25]; marmots: [24]; red deer: [26]), and hence, could not control for potentially covarying acoustic parameters (e.g., f_o, intensity). It thus remains crucial to understand the biological function(s) of each type of NLP by testing their independent perceptual effects across different species, call types, and behavioural contexts. Yet, until recently, a major limitation in the experimental study of NLP has been the absence of tools to synthesise naturalistic sounds with controlled levels of NLP.

Here, we take advantage of recent advances in parametric sound synthesis, thus far used only on human nonverbal vocalisations [18,31,32], to systematically add NLP to synthetic, yet highly realistic, nonhuman animal vocalisations. More specifically, we applied this method to investigate how the presence and duration of NLP in distress whines, produced by 1- to 9-week-old domestic dog puppies, affect their perception by humans. Whines are high-pitched tonal calls considered to signal distress, typically given by puppies during separation [33] or aggression by their mother [34]. Like adult dog whines [11,12], puppy whines also often contain NLP (see electronic supplementary material), particularly when the dog's emotional arousal increases (personal observation). Although puppies' survival mainly relies on mothers, who intensively breastfeed, groom, and warm them [34], the intervention of human caregivers is sometimes required for breeding in this domesticated species [35]. As such, NLP in whines may be important to attract the attention of the mother, but also of humans, ensuring that puppies receive care. Indeed, the common presence of NLP across vertebrate infant distress calls suggests that these shared vocal features may support the interspecific vocal communication of need to human caregivers [22]. Therefore, to investigate the possible function of NLP as vocal indicators of distress in human-puppy interactions, we performed playback experiments using synthetic puppy whines in which we manipulated the presence, and duration, of NLP (frequency jumps, subharmonics, sidebands, chaos) across f_o levels (low, medium, high). We predicted that NLP added to whines, particularly chaos, would increase human perceptions of the puppy's distress, and that higher proportions of NLP would enhance these perceptual effects. Moreover, because NLP affect perceptions of size and dominance in synthetic human vocalisations [18,32], we tested whether these perceptual effects generalize to other mammal vocalisations. Indeed, dominance-like behaviours have been described as a trait of individual temperament in dogs [36,37], and can occur during the early development of pre-weaned canids, including puppies (e.g., during play with littermates) [36,38]. We thus predicted that NLP would increase perceived size and dominance. Finally, under the assumption that the interspecific function of infant distress vocal signals may be particularly important in caregiving contexts (e.g., for breeders and veterinarians), we replicated our experiment on a distinct sample of professionals with extensive experience in puppy caregiving to test whether such experience modulates the perceived effects of NLP.

Materials and Methods

Our experimental protocol included: (1) audio recording natural distressed puppy whines, (2) creating synthetic whine stimuli based on these recordings of natural vocalisations, and (3) online playback experiments in which we respectively tested 200 and 217 human listeners from the general population (Experiments 1 and 2), and 55 listeners selected for their extensive experience in puppy caregiving (Experiment 3). All participants judged the perceived level of distress, body size, and dominance conveyed by each synthesized puppy whine. While the first and third playback experiments tested the perceptual effects of the presence or absence of NLP, the second experiment also tested the perceptual effects of their duration (Table 1).

	Playback Experiment 1 (N=200) and Experiment 3 (N=55)	**Playback Experiment 2 (N=217)**
Total number of original synthetic prototypes	20	40

Manipulations	Types of NLP	none, frequency jumps, subharmonics, sidebands, chaos	none, subharmonics, sidebands, chaos
	Duration of NLP (% of whine duration)	20-40%*	50% or 80%
	Levels of f_o	low, medium, high	low, medium, high
Total number of synthetic stimuli		300	840

Table 1: Overview of the experimental design used for playback experiments. Level of manipulation 'none' indicates vocal stimuli without NLP. * Values drawn at random within this range, derived from the peak of the observed distribution of NLP durations. Experiments 1 and 3 shared an identical design and identical whine stimuli.

Acoustic recordings

We recorded whines of 32 Beagle puppies from 6 different litters at roughly 1-, 3-, 6-, and 9-weeks of age (Table S1) at two different breeding facilities (France). We used a Sennheiser MKH70 directional microphone connected to an audio recorder Zoom H4n (44.1kHz, 24bit) and positioned at approximatively 30 cm from the animal's mouth.

Mothers and their litter stayed in the same enclosure during the 9 first weeks of the puppies' lives. To record natural whines, each puppy was placed alone in a pen in a separate room (roughly 100 x 50cm). Each puppy was thus recorded in a separation behavioural context, without visual and acoustic contact with its mother and littermates. This method of recording distress vocalisations has been widely applied in vertebrates [22]. Our recordings started once the puppy had produced its first whine and did not last for more than 5 minutes to limit stress potentially induced by our experimental conditions. At the breeding facilities, bitches are habituated to being temporarily separated from their litter (e.g., during daily walks) and accustomed to breeders manipulating puppies during daily care (e.g., weight measurements evaluating physical condition of puppies). It was thus unlikely that we induced stressful behaviours in mothers while recording their puppies. In addition, when bringing the puppy back to its mother, the observation of normal maternal behaviours such as grooming or breastfeeding [34] indicated low stress levels.

Stimulus creation

From this pool of acoustic recordings of natural puppy vocalisations, we used 10 whine sequences at each age category (i.e., 1-, 3-, 6-, 9- week-old, 40 sequences in total) from 26 different individuals as templates to create their associated fully synthetic copy (hereafter synthetic prototype). We choose whine sequences composed of three repeated whines without NLP to facilitate their synthesis with the R package *soundgen* [31].

For each synthetic prototype, we prepared sets of vocalisations with systematic manipulations of NLP and f_o (Table 1) for playback experiments. Specifically, we created synthetic whine stimuli at low, medium, and high levels of f_o, with or without different types of NLP added at each f_o level, based on those that naturally occur in puppy whines, including frequency jumps or varying proportions of subharmonics, sidebands, and chaos (Fig. 1). Manipulations of NLP and f_o were applied to the three repeated whines composing the entire synthetic prototype.

To inform these manipulations, we first performed detailed acoustic analyses on our recorded whines to characterise the natural vocal variation in puppy whines (see electronic supplementary material). We manually measured onset time and proportion of NLP as well as the f_o of 4841 natural whines containing NLP. This allowed us to create highly realistic variants that remained within the range of natural production, thus increasing the ecological validity of our experimental method and reliability of our results.

In total, there were 300 stimuli in Experiments 1 and 3: 20 prototypes * 5 NLP conditions (none, frequency jump, subharmonics, chaos, sidebands) * 3 f_o levels (low, medium, high). Experiment 2 included 840 stimuli: 40 prototypes * 7 conditions of NLP duration (none + 50% or 80% of the whine duration affected by subharmonics, sidebands, chaos = 1+ 2*3 = 7) * 3 f_o levels. All audio stimuli and R code for their synthesis are available for download at https://osf.io/rp7m8/.

1- *Manipulations of nonlinear phenomena*

Experiments 1 and 3 tested perceptual effects of the presence or absence of NLP in puppy whines. We manually coded frequency jumps as instantaneous changes in f_o occurring at the maximum f_o slope. Indeed, as the production of NLP is typically associated with increases in subglottal pressure, leading to a relatively high f_o and amplitude, and ultimately, to an unstable vocal system [3,39], NLP are expected to occur in sections of calls where f_o is relatively high [40]. We also added sidebands, subharmonics, and chaos to whines by randomly selecting the onset time from the observed natural distribution. Durations of these types of NLP were selected at random within an interval corresponding to the most commonly produced NLP durations in natural whines, i.e., 20% to 40% of the whine's duration (Fig. S1).

Experiment 2 tested perceptual effects of NLP duration. Here, the duration of NLP was fixed at either 50% (hereafter medium proportion) or 80% (hereafter high proportion) of the variant's duration (Fig 1.a), both of which remained within the natural range (Fig. S1). The onset time of NLP was also randomly selected from the observed natural distribution, but under the constraint that the onset time should be within a specific interval (medium proportion: [0; 50] % of the whine duration, high proportion: [0; 20] % of the duration).

We synthesized subharmonics, sidebands, and chaos using a method allowing for natural variability. Specifically, to synthesise subharmonics, the integer ratio of subharmonic frequencies to f_o was drawn from a truncated Poisson observed distribution (mean=1 and range= [2, 5]), typically resulting in additional spectral components (subharmonics) at $f_o/2$ or $f_o/3$. We created sidebands by adding amplitude modulation, the frequency of which was selected from a Gaussian distribution (mean ± SD = 170 ± 20 Hz) characterizing sidebands in natural puppy whines. The amplitude of subharmonics and sidebands, expressed as the proportion of the amplitude of f_o, was randomly selected from a Gaussian distribution with a mean ± SD of 50% ± 10% [3] and 80% ± 10%, respectively. Finally, we created chaos by adding jitter (i.e., changes in f_o periodicity) with values of 3 ± 0.6 semitones in Experiments 1 and 3, and 1.2 ± 0.3 semitones in Experiment 2, such that chaotic episodes sounded natural.

2- Manipulations of f_o

Because variations in f_o can affect perceptions of distress [41–44], size [45,46], and dominance [47], we also tested whether perceptual effects of NLP vary across f_o levels. From our f_o measurements of natural whines containing NLP, we identified three main f_o categories that roughly correspond to quartiles of the natural distribution with a mean ± semitones/2 of 790 ± 27 Hz (low f_o), 972 ± 27 Hz (medium f_o), and 1170 ± 27 Hz (high f_o), hereafter termed target region. We thus synthetised stimuli at each f_o level by first randomly selecting a target f_o value from each target region. This allowed for natural variability in f_o across variants within each target region. Second, we calculated a coefficient of correction as the ratio between the target f_o value and average f_o across whines in the original synthetic prototype. Third, the f_o of the prototype was corrected by this coefficient, such that the average f_o of the new variant reflected the target f_o value.

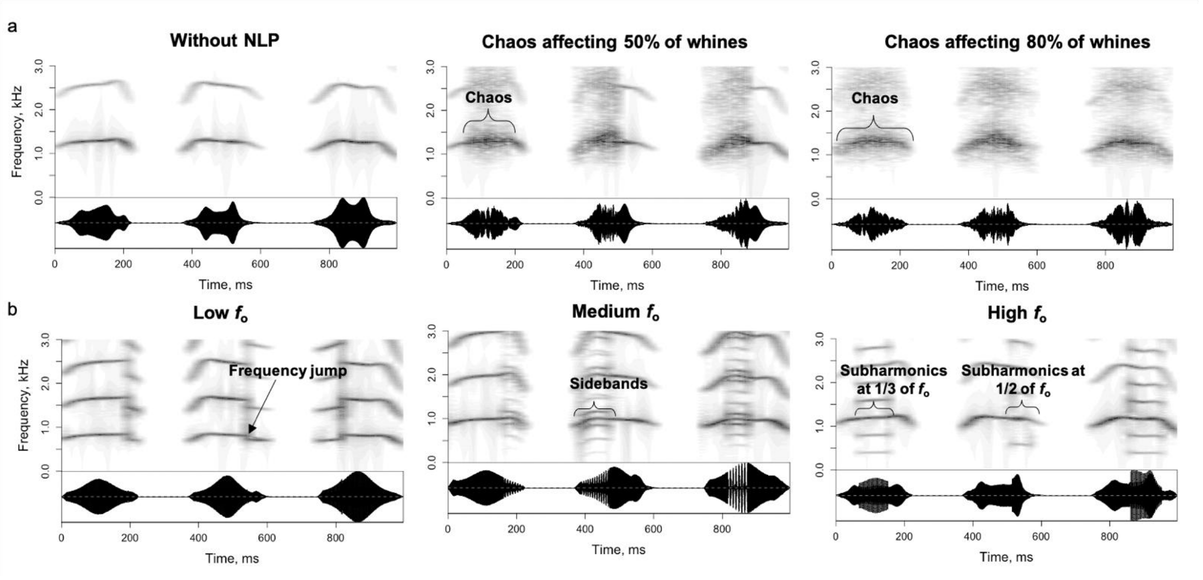

Figure 1: Spectrograms of variants of the same whine prototype synthesized with or without NLP (frequency jumps, subharmonics, sidebands, chaos) at different levels of (a) NLP duration (NLP affecting 50% or 80% of the whine's duration, as illustrated with the addition of chaos) and (b) f_o (low, medium, high). While every NLP manipulation was tested at every f_o level, here we show a range of NLP manipulations at each f_o level as examples.

Playback experiments with human listeners

We performed online playback experiments on 487 human adult listeners (*N*= 206 Experiment 1; *N*= 221 Experiment 2; *N*= 55 Experiment 3). Before each experiment, participants completed a short questionnaire indicating their sex, age, profession, level of comfort with puppies and experience with puppy-ownership. They were also informed that they would hear distressed puppy whines recorded during separation from mothers and littermates. Because the term "puppy" can refer to both pre- and post-weaned dogs, we defined a puppy as a dog younger than 3 months of age in our online questionnaire. Participants first listen to three natural whine sequences containing NLP to familiarise themselves with nonlinear puppy whines and to adjust their sound level to a comfortable volume, which was then kept constant for the experiment. We asked participants to use headphones when completing the experiment in a quiet environment.

Playback experiments comprised three blocks testing perceived distress, size, or dominance. The order of blocks and stimuli within blocks were randomized. Each block contained 20 (Experiments 1 and 3) or 40 (Experiment 2) whine stimuli, such that each prototype was tested once per block with a randomly chosen level of f_o and NLP condition for a given participant who listened to a total of 60 stimuli (Experiments 1 and 3) or 120 stimuli (Experiment 2). Following each whine exposure, participants rated the whine by indicating how distressed/dominant/large the puppy sounds, using a continuous sliding scale ranging from 0 (Not at all distressed/dominant or extremely small) to 100 (Extremely distressed/dominant/large). Participants could listen to stimuli several times and could adjust their rating if needed.

In Experiments 1 and 2, we respectively excluded 6 and 4 participants who completed less than 80% of the experiment or otherwise failed to engage with the study. No participant from Experiment 3 was excluded. Statistical analyses were thus performed on 472 participants (*N*= 200 Experiment 1, *N*= 217 Experiment 2, *N*= 55 Experiment 3), aged 28 ± 11 years old (mean ± SD) (range [18-74]), of whom 40% self-reported as female, 60% as male, and less than 1% as 'other'. Nearly all participants in Experiments 1 and 2 (409/417) did not professionally work with puppies but felt comfortable in their presence (381/417), and 65% had owned a puppy within the past 5 years. In Experiment 3, we specifically selected participants for their extensive experience in puppy caregiving, and thus their regular exposure to whines. Most of these participants professionally worked with puppies, as out of 55, 40 were dog breeders, 12 were veterinarians, and 2 were dog trainers.

Data analysis

Data from playback experiments were analysed using Bayesian multilevel models fitted with the *brms* R package [48] using default priors. The response variable of models corresponded to ratings re-coded from 0 to 1 and modelled with zero-one-inflated beta distribution [49].

To investigate whether the presence of NLP affected human perceptions of puppy whines, and whether these effects of NLP varied with whine f_o, we first fitted a model including data from Experiments 1 and 2, testing the general population (N=417 participants). This model included a three-way interaction between the tested perceptual scales (3 levels), NLP condition (5 levels) and f_o (3 levels). We allowed effects of NLP on each scale to vary across participants and prototypes by fitting the interaction between NLP and scale as random slopes for all participants and prototypes. We also assumed that each stimulus would have its unique rating on each scale. This model resulted in the following *brms* syntax:

Rating response ~ scale*NLP*f_o + (NLP * scale|participant) + (NLP * scale|prototype) + (scale|stimulus)

To examine whether experience in puppy caregiving influences the effects of NLP, we fit an analogous model to the data collected from experienced caregivers (*N*=55 participants in Experiment 3). Finally, we tested whether the duration of NLP reinforced their perceptual effects by fitting a second model with data from Experiment 2 (*N*= 217 participants). This model included a two-way interaction between rating scales and duration of NLP (7 levels). The model followed this *brms* syntax:

Rating response ~ scale*duration + (scale*duration| participant) + (scale*duration|prototype) + (scale|stimulus)

In this model, we captured an assumed variability of predictors *scale* and *duration* across participants and prototypes and allowed for ratings of each scale to vary across each unique stimulus. Posterior distributions of model parameters were summarized by their median and 95% credible interval.

Results

We predicted that the presence and duration of NLP in puppy whines would increase perceptions of distress, size, and dominance by human listeners. With the exception of frequency jumps, all NLP affected listeners' ratings on one or more of these perceptual scales (Fig. 2.a, Fig. 3, Fig. S2.a).

Specifically, in the general population (Experiments 1 and 2), we found that perceptions of distress were primarily affected by chaos, which increased distress ratings by 5.6% [3.8, 7.4] compared to identical whines without NLP. In contrast, distress ratings were not noticeably affected by the addition of subharmonics (-0.7% [-2.1, 0.7]) nor sidebands (1.3% [0, 2.6]). Experienced puppy caregivers (Experiment 3) also rated whines with chaos as more distressed-sounding, but unlike the general population, they furthermore associated sidebands and subharmonics with higher distress (see electronic supplementary material for details, Fig. S2.a).

Moreover, we predicted that longer episodes of subharmonics, sidebands, and chaos in puppy whines would increase their perceptual salience and thus, enhance their effects on perceived distress. Surprisingly, we found that increasing the duration of chaos from 50% to 80% of the whine’s duration did not further increase perceived distress (-0.4% [-3.0, 2.3]), and that increasing the duration of subharmonics and sidebands reduced perceived distress by 4.8% [2.2, 7.5] and 3.1% [0.8, 5.4], respectively (Fig. 3).

While effects of NLP were relatively stable across each f_o level, our results confirm an independent effect of f_o on distress ratings in participants for all three experiments (Fig. 2.b and c; Fig. S2.b and c). Indeed, puppies producing whines with higher levels of f_o were rated as more distressed (9.3% [8.1, 10.6]), compared to the same whines synthesized at lower f_o levels (Fig. 2b).

In addition to effects on perceived distress, our results show that the general population (Experiments 1 and 2) rated size and dominance about 4% to 6% higher in whines containing subharmonics, sidebands, or chaos, compared to whines without NLP (Fig. 2.a). However, these effects were absent or limited in experienced puppy caregivers (Fig. S2.a).

We also predicted that increasing the duration of subharmonics, sidebands, or chaos from 50% to 80% of the whines’ durations would reinforce their effects on perceived size and dominance. Our results indeed show that whines containing 80% of subharmonics (but not chaos and sidebands) increased perceived size by 6% [3.0, 8.9] and perceived dominance by 5.1% [2.3, 7.7] compared to the same whines with only 50% of these NLP (Fig. 3).

Finally, we found no interactions between NLP and f_o levels in the general population (Fig.2c), instead confirming an independent effect of f_o on perceived size and dominance (Fig.2b): whines with a lower f_o were systematically associated with larger (12.9% [14.1, 11.7]) and more dominant (5.9% [-7, -4.8]) sounding puppies, relative to the same whines synthesized at higher levels of f_o. Similar results were found for experienced puppy caregivers (Fig. S2.b and c).

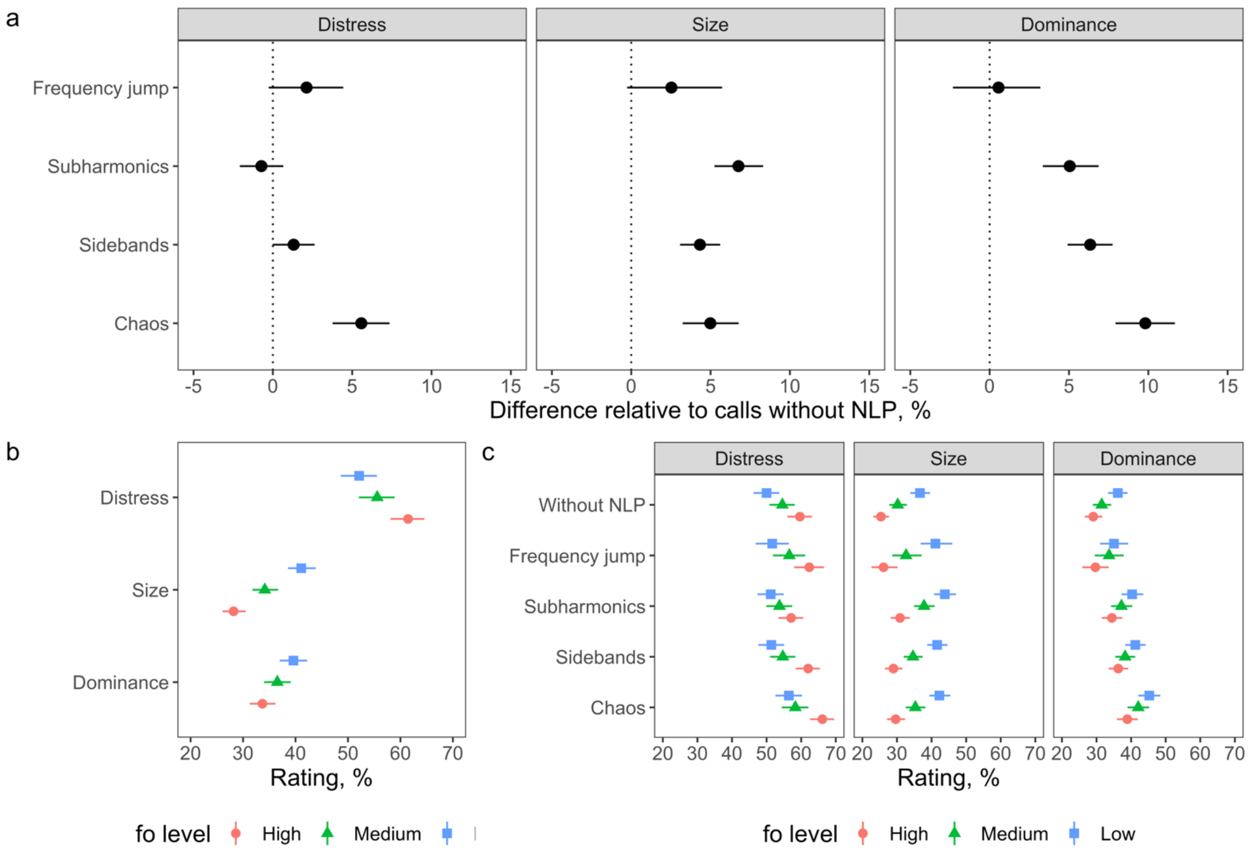

Figure 2: Main effects of (a) NLP, (b) f_o, and (c) interactions between NLP and f_o on perceived distress, size, and dominance (N=417, Experiments 1 and 2). Solid markers correspond to medians of posterior distribution with their 95% credible intervals.

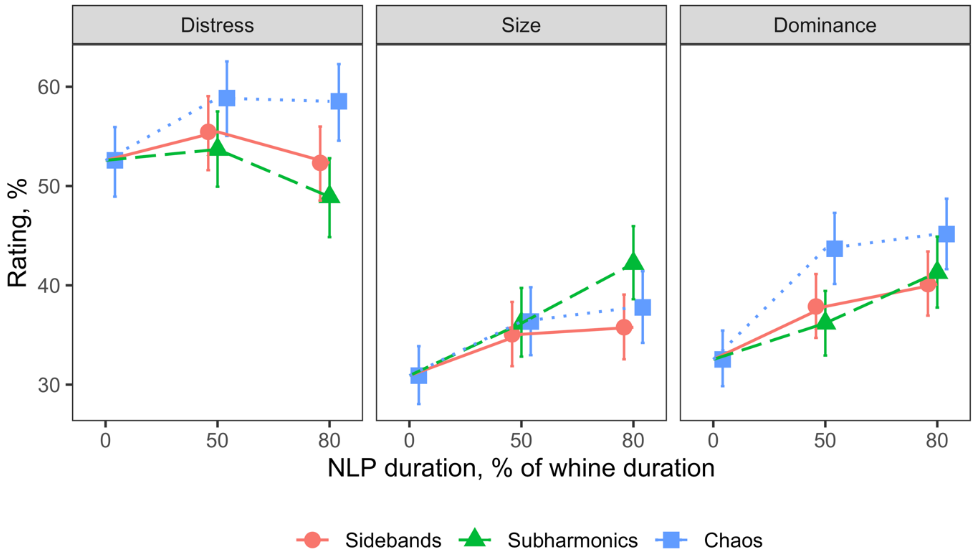

Figure 3: Effects of NLP duration on perceived distress, size, and dominance in Experiment 2 (N=217). A duration of zero corresponds to whines without NLP. Solid markers correspond to medians of posterior distribution with their 95% credible intervals.

Discussion

We investigated the independent perceptual effects of nonlinear phenomena (NLP) that occur naturally in a non-human animal vocalisation, namely in distressed puppy whines. By applying an innovative method of parametric sound synthesis in the context of interspecific vocal communication, we show that the presence and duration of different NLP types in puppy whines generally increase their perceived distress, size, or dominance, as judged by human listeners.

Deterministic chaos increases perceptions of distress

We found that the presence of chaos in puppy whines, but not the addition of frequency jumps, sidebands, or subharmonics, increased perceptions of distress in human listeners representing the general population. From a biomechanical perspective, the production of NLP, particularly chaos, is typically associated with high subglottal pressure and strong muscle tension on vocal folds [39] - configurations of the vocal apparatus that are likely to arise in distressed animals with highly aroused physiological states [1]. Chaos is indeed a characteristic of calls associated with distress in a wide range of mammals ([10,15,16,21,23], this study). Additionally, at the perceptual level, Blumstein and Récapet (2009) [24] have shown that white noise (which shares some perceptual elements with deterministic chaos [50]) added to natural alarm calls of marmots induces potentially costly responses in these animals (reduced foraging activity). An earlier study also showed that chaos added to human nonverbal vocalisations increases the intensity of perceived negative, rather than positive, affective states [51]. Together, our findings thus support that chaos is perceived as a vocal indicator of higher levels of distress in mammals.

As increases in subglottal pressure, characterised by high amplitude and f_o, often lead to vocal instability [3,39], NLP are expected to occur when f_o is relatively high. For instance, the onset of NLP corresponds with the maximum f_o in chimpanzees' calls [40]. As such, it is difficult to disentangle the effect of f_o from the effect of NLP when performing playback experiments using natural calls [9,24,25], as these acoustic parameters may covary. To overcome this limitation, we used synthetic stimuli varying in the presence and duration of NLP at different f_o levels. While we confirmed that perceived distress increases independently with f_o, as reported in numerous previous studies [41–44], the effect of NLP on the perception of distress was relatively stable across all f_o levels. This suggests that perceptual effects of f_o and NLP are independent and cumulative, and that both are salient vocal indicators of distress.

Contrary to our prediction, whines containing relatively longer episodes of chaos did not increase perceived distress compared to whines with less chaos, suggesting that a ceiling effect may have been attained with chaos affecting only half of the call duration. Indeed, listeners may have applied a categorical decision (no chaos = relatively low distress, chaos = relatively high distress) when exposed to whines with or without chaos. Moreover, for sidebands and subharmonics (whose presence did not affect perceived distress in the general population), we found that perceived distress was lower in variants containing longer episodes of these NLP. We suggest that bifurcations between the tonal and non-tonal sections of the calls may be less salient in calls with a largely dominant non-linear regime. In a recent study, we showed that subharmonics and sidebands added to human nonverbal vocalisations lowered their perceived pitch [18]. As such, when exposed to subharmonics or sidebands affecting 80% of the whine duration, listeners may have perceived these calls with a relatively high tonality at a lower f_o and may thus have associated these lower-pitched sounds with behavioural contexts of aggression, rather than distress. This would follow Morton's motivation-structural rules stating that aggressive animals typically produce low-pitched sounds, whereas distressed, fearful animals produce high-pitched sounds [28].

Nonlinearities increase perceptions of size and dominance

Experimentally adding subharmonics, sidebands, and chaos - but not frequency jumps – to whines increased the puppy's perceived body size and dominance. Increasing the duration of subharmonics further increased perceived size and dominance. These results are consistent with recent work on human nonverbal vocalisations [18,32]. Our results also confirm the well-established perceptual effect of f_o on size and dominance [45–47] – whines with a relatively low f_o were systematically perceived as produced by larger and more dominant-sounding puppies, independent of the effects of NLP on perceived size and dominance. Although we show that f_o directly affects perceptions of size and dominance, we cannot completely rule out the possibility that NLP independently lower the perceived pitch of whines (as they do in human vocalisations) [18]. This pitch-lowering effect may thus be one of the perceptual mechanisms whereby NLP cause puppies to sound larger and more dominant. This prediction could be directly tested in future work by simultaneously assessing the effect of NLP manipulations on auditory (pitch, timbre) and ecological (distress, dominance, etc.) dimensions.

The pitch-lowering effect of NLP has been hypothesised as a possible strategy for animals to exaggerate perceived size and dominance [4,5]. Indeed, frequency components such as formant frequencies and/or f_0 mediate the vocal communication of size and dominance, which are crucial factors affecting the outcome of social interactions, such as mating, sexual competition, or territorial defence [2]. Many species have developed strategies to exaggerate their apparent size and, potentially, also their dominance (reviewed in [27] and [52]), with specific adaptations to their vocal apparatuses such as a descended and mobile larynx [53]. Because there is no clear biological function for a puppy to sound larger and more dominant to humans while producing a distress vocalisation, we suggest here that the perceptual effects of NLP on size and dominance are likely the consequence of a general perceptual bias linking “*harsh”* with “*large and dominant”* [18].

Effect of experience on listener perception of puppy whines

While infant distress calls conveying need to parents are ubiquitous in vertebrates [22], in the context of domestication, these distress calls may also function to communicate need to heterospecific caregivers. Indeed, human baby pain cries are often characterised by very high levels of NLP [16] and human listeners pay attention to these acoustic features to assess a baby’s level of distress and need [16]. As such, the production of whines, and within them the production of NLP, may have been encouraged by dog domestication, with puppies exploiting human sensitivity to chaos in offspring calls. Breeders indeed do intervene and provide care to puppies [35], e.g. in the case of mother neglect, aggression, or rejection [34]. Consistent with this, when asked to characterise how they react when exposed to puppy whines in their normal professional activities, more than 50% of our experienced puppy caregivers reported being negatively affected by whines, paying attention to their harshness and roughness, and using these acoustic features as cues to distress in order to adjust the level of care they provide to the puppies. Interestingly, while experienced caregivers were as sensitive to chaos as the general population when rating perceived distress, they also associated subharmonics and sidebands with higher levels of distress (unlike the general population), as also observed in other species (e.g., subharmonics in meerkats: [9]). Together these results suggest that human sensitivity to chaos, the most severe form of NLP, has a universal base when assessing distress in puppy whines, but that sensitivity to other NLP can also arise with extensive experience. To further investigate the possibility that domestication may have emphasised whining and NLP within puppy whines as a consequence of sensory exploitation of caregivers (or as a consequence of relaxed predation pressures [54]), future studies should contrast the production of NLP within the whines of domestic dog puppies and wolf pups (*Canis lupus*).

Finally, NLP had little effect on perceptions of size and dominance in experienced caregivers, suggesting that their extensive experience allows them to correct for the perceptual bias identified in our general population. At the same time, experienced caregivers remained sensitive to whine f_0 when assessing distress, size and dominance. This suggests that f_0 may function as a reliable index of these traits in puppy vocalisations, as identified for distress and size in adult dog whines [55,56]) and in the calls of other mammals [1,2], a hypothesis that we are currently investigating.

Perspectives

It remains to be established whether NLP signal distress information in puppy-mother vocal interactions, as they do to human listeners. Indeed, a recent study reports a positive relationship between the level of jitter (“noisiness”) in natural distress puppy whines and the strength of adult dogs’ behavioural responses [57]. Furthermore, although whines are typically associated with distress contexts, the domestic dog’s vocal repertoire also includes vocalisation types that are produced in both positive (e.g., playful) and negative (e.g., agonistic) contexts, such as growls or barks [58,59]. In addition to signalling relatively stable physical attributes (e.g., size) [60], these vocalisations can vary acoustically between positive and negative behavioural contexts [56,61]. For example, high-pitched and tonal barks are produced in playful contexts whereas low-pitched and harsh, chaotic barks are more commonly produced during territorial defence [56]. Nonlinear phenomena in barks or growls may thus function to communicate aggressive intent (rather than play) and, in such an agonistic context, may also function to exaggerate size and dominance. This prediction may be tested in the contexts of both inter- and intra-specific vocal communication. We thus suggest that using methods of parametric sound synthesis, as reported here, could be generalised to a wider range of species and contexts to directly test the communicative function of NLP in animal vocal communication.

Ethics

Acoustic recordings of puppies were performed under the ethical Approval no. E-42-218-0901 (ENES lab agreement, Direction Départementale de la Protection des Populations, Préfecture du Rhône). All human participants provided informed consent, and ethical approval for performing perceptual experiments with human subjects was provided by the Comité d'Ethique du CHU de Saint-Etienne (IRBN692019/CHUSTE).

Data accessibility

All audio stimuli, R codes for synthetizing stimuli, html code for running psychoacoustic experiments, datasets as well as R codes for analysing data can be downloaded from https://osf.io/rp7m8/.

Author's contributions

All authors designed the study. M.M. collected the data; M.M. and A.A. created the stimuli and performed the data analyses; M.M. wrote the original draft. All authors reviewed and edited the manuscript and gave their final approval for publication; D.R. Supervised the study.

Competing interests

The authors declare no competing interests.

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