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Vocal modifications in primates: Effects of noise and behavioral context on vocalization structure

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Abstract

During increased noise, modifications of the acoustic structure of vocalizations (amplitude, temporal, and spectral parameters) may allow release from masking, potentially conferring fitness benefits to vocally flexible signalers. Among primates, humans have demonstrated extreme vocal flexibility during noise, with modifications to all three speech parameters affected by both noise type and motivational state of the signaler. While non-human primates have also demonstrated changes to call amplitude and temporal characteristics, to the best of our knowledge spectral modifications have not been observed and the influence of behavioral context remains unknown. This experiment used playbacks of broad (10 kHz) and narrowband (5 kHz) white noise to investigate the effects of noise level and bandwidth on chirps and combination long calls (CLCs) produced by cotton-top tamarins (*Saguinus oedipus*). Noise amplitude and frequency content both influenced the structure of vocalizations; modifications included increased call amplitude (the Lombard effect), changes to call durations, and previously undocumented spectral shifts. Behavioral context was also relevant; modifications to CLCs were different from those observed in chirps. These results provide the first evidence of noise-induced spectral shifts in non-human primates, and emphasize the importance of behavioral context in vocal noise compensation.

INTRODUCTION

Noise is known to exert a significant influence on the evolution of acoustic communication, imposing fitness costs on animals that lose contact with offspring, miss mating opportunities, or do not hear alarm calls from group members. Short-term variability in ambient noise (ranging from milliseconds to days) due to weather events, animal choruses, or other environmental factors, can overlap the range of signalers' evolved communication frequencies and potentially disrupt communication. Short-term (seconds to days) changes to the acoustic environment may select for vocal flexibility in signaling animals, potentially allowing signalers to compensate for increased noise by changing either their calling behavior or the acoustic characteristics of their signals.

Changes that result in a modification of the acoustic structure of a signal are termed noise-induced vocal modifications (NIVMs; Hotchkin and Parks, In press), and may affect call amplitude, frequency, or temporal parameters. The amount of flexibility in signal production varies between species, with some taxa capable of modifying all signal dimensions, while

others are restricted to changing only amplitude or duration of signals (Lesage *et al.*, 1999; Egnor and Hauser, 2006; Tressler and Smotherman, 2009; Love and Bee, 2010). Interestingly, while humans are among the most vocally-flexible species known, non-human primates appear to have significantly less control over the structure of their acoustic signals (Fitch, 2000; Egnor and Hauser, 2006; Snowdon *et al.*, 2009).

Different types of NIVMs may be more effective at increasing signal detectability during noise with particular spectral or temporal characteristics. For instance, in the case of relatively continuous low-frequency noise, either increasing call amplitude or shifting call frequency out of the noise may increase signal detection. Noise characteristics have been shown to differentially affect vocal modifications in human speech (Egan, 1972; Garnier *et al.*, 2010), and are an important factor to consider in evaluating NIVMs in non-human species.

As noted by Lane and Tranel (1971), a signaler's motivation and behavioral context may also significantly affect the acoustic structure of vocalizations. Social factors, emotional status, and behavioral state have been shown to affect the spectro-temporal structure of vocalizations in humans and non-human mammals (Lane and Tranel, 1971; Miksis-Olds and Tyack, 2009; Garnier *et al.*, 2010; Briefer, 2012). However, the interactions of noise and behavioral context on the acoustic structure of vocalizations produced by non-human mammals have not yet been thoroughly examined. This study examined the effects of noise on two types of vocalizations produced by cotton-top tamarins (*Saguinus oedipus*) in different behavioral contexts.

Cotton-top Tamarin Vocalizations

Previous studies have indicated that non-human primates are capable of modifying the amplitude and temporal structure of their vocalizations during increased noise (Brumm *et al.*, 2004; Egnor and Hauser, 2006; Egnor *et al.*, 2006), but seem to lack the ability to modify spectral parameters (Egnor and Hauser, 2006; Snowdon *et al.*, 2009). In species with extensive vocal repertoires, including cotton-top tamarins (Cleveland and Snowdon, 1982), the behavioral contexts in which sounds are produced may also affect the types and intensity of NIVMs. In captive groups, when individuals are removed from a colony, the focal individual or other animals in the colony will often spontaneously produce a multi-syllable, stereotyped vocalization known as the 'combination long call' (CLC), which consists of "chirp" and "whistle" syllables, and appears to function as a long-distance contact call (Cleveland and Snowdon, 1982). This call type is also produced in response to other individuals producing CLCs ('antiphonal calling'); perceptual characteristics of the call type are well known, and informationally important components have been identified (Weiss *et al.*, 2001; Weiss and Hauser, 2002; Jordan *et al.*, 2004).

Behavioral functions for other types of tamarin vocalizations, including the second call type examined in this experiment (chirps), are not as well understood. Cleveland and Snowdon (1982) described the behavioral functions of several types of chirps produced by wild tamarins; these functions appear to be consistent in chirps produced by captive populations (Castro and Snowdon, 2000). The chirps produced in this experiment appear to be similar to

Cleveland and Snowdon's type E vocalization, produce in response to visual or auditory stimuli.

PLAYBACK EXPERIMENT

A playback experiment was used to investigate the effects of two noise parameters (level and bandwidth) on the acoustic structure of cotton-top tamarin vocalizations. Data were collected between November 2011 and March 2012. The animals used for this study were housed in a single colony on the main campus of The Pennsylvania State University, University Park, PA. Animals were fed a standard tamarin diet of monkey chow, seeds, nuts, and fruits with ad libitum access to water. The design of the colony room allowed unlimited acoustic contact by all colony members and limited visual contact with animals in neighboring home cages. Seven animals were tested in this study; of these, two did not vocalize during trials and were excluded from analysis, yielding an effective sample size of five (3 male, 2 female).

Test sessions consisted of one control (silent) and one treatment (noise) trial presented in random order with a 15 – 60 minute rest period between trials. White noise playback stimuli were generated in Adobe Audition© version 5, and band-pass filtered to generate six bandwidth and level combinations (Table 1). Noise bandwidths and frequency ranges were selected to target the masking noise at the perceptually important second harmonic of CLCs (Weiss and Hauser, 2002). Broadband stimuli contained energy between 100 Hz and 10 kHz; narrowband stimuli ranged from 1.5 kHz to 6.5 kHz. CLC production was encouraged by eliciting antiphonal calling to playbacks of CLCs from an unfamiliar adult tamarin ('elicitation stimuli').

Each trial began with a two-minute acclimation period during which no call elicitation stimuli were played. The test period began immediately after the two minute acclimation period was complete. If the subject had been spontaneously producing CLC vocalizations during the acclimation period, the experimenter waited 60 seconds to see if the animal would continue vocalizing spontaneously. If no CLCs were produced within that time, then call elicitation stimuli were played in random order at approximately 30 second intervals to elicit response calling from the subject. If no spontaneous CLCs were produced during the acclimation period, elicitation stimuli playbacks began within 15s of the end of the acclimation period, and were repeated in random order when the focal animal was silent for 30 seconds for the duration of the test period.

The test period continued until the animal had produced 5 high SNR CLCs, or 10 chirps, or until the total noise exposure (including acclimation period) reached 12 minutes. If the animal did not produce the required number of vocalizations, the data were discarded and the trial was re-run on another day. At the end of the first trial, the animal was removed from the test cage and returned to its home cage for a 15 – 60 minute rest period before the second trial. The test cage was sanitized with Quatricide® PV after each trial.

Statistical analyses were performed in SAS version 9.2. Call parameters (amplitude, duration, and frequency measurements) were averaged for all same-type vocalizations produced by a subject during each trial, giving a total of 6 paired treatment-control data

points per subject. Analysis of covariance (ANCOVA) models were generated to determine the effects and interactions of noise level and bandwidth on source level, peak frequency, minimum frequency, and duration of both call types. Noise level was treated as a continuous variable and subject identity was included as a random effect.

CONTEXT-DEPENDENCY OF VOCAL MODIFICATIONS

Of the five individuals tested, three subjects reliably produced CLCs, and two produced chirp vocalizations. Only one subject (Bart) produced both chirps and CLCs. Different suites of vocal modifications were observed in CLCs and chirps. Most notably, there were no changes to the duration of CLCs, while chirp duration increased significantly during higher noise levels. The Lombard effect was observed for both call types, but was more pronounced in CLCs than in chirps. Spectral parameters also changed for both call types; peak frequency increased for both call types, but the driving mechanism for this change appeared to differ between CLCs and chirps. Changes to spectral tilt (energy distribution within a call) were detected for CLCs, but not chirps.

Our results provide the first evidence for noise-induced spectral shifts in non-human primate vocalizations, the first experimental demonstration of shifts in spectral tilt in a non-human species. and emphasize the importance of behavioral context in vocal noise compensation. These findings suggest greater evolutionary continuity in vocal control between nonhuman primates and humans than previously supposed. Consistent with results from other species, noise-induced vocal modifications in tamarin calls appeared to vary with either behavioral context or the signaler's need for social contact (Lane and Tranel, 1971; Miksis-Olds and Tyack, 2009; Tressler and Smotherman, 2009; Garnier *et al.*, 2010). It is possible that tamarins that intend to communicate over long distances may expend more energy in changing the structure of vocalizations during increased noise than animals expressing alarm or needing communicate over a short distance. Alternatively, differences in call structure between chirps and CLCs may influence the flexibility of certain call parameters in increased noise. Future studies of the behavioral function of chirps and of the effects of noise on tamarin vocalizations will be provide more insight into the interactions of behavioral context and vocal noise compensation.

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REFERENCES

- Briefer EF. Vocal expression of emotions in mammals: mechanisms of production and evidence. *Journal of Zoology*. 2012
- Brumm H, Voss K, Kollmer I, Todt D. Acoustic communication in noise: regulation of call characteristics in a New World monkey. *J Exp Biol*. 2004; 207:443–448. [PubMed: 14691092]

- Castro NA, Snowdon CT. Development of vocal responses in infant cotton-top tamarins. *Behaviour*. 2000;629–646.
- Cleveland J, Snowdon CT. The Complex Vocal Repertoire of the Adult Cotton-top Tamarin (*Saguinus oedipus*)1). *Zeitschrift für Tierpsychologie*. 1982; 58:231–270.
- Egan JJ. Psychoacoustics of the Lombard voice response. *J. Aud. Res.* 1972; 12:318–324.
- Egnor SER, Hauser MD. Noise-induced vocal modulation in cotton-top tamarins (*Saguinus oedipus*). *American Journal of Primatology*. 2006; 68:1183–1190. [PubMed: 17096420]
- Egnor SER, Iguina CG, Hauser MD. Perturbation of auditory feedback causes systematic perturbation in vocal structure in adult cotton-top tamarins. *J Exp Biol*. 2006; 209:3652–3663. [PubMed: 16943505]
- Fitch WT. The evolution of speech: a comparative review. *Trends in Cognitive Sciences*. 2000; 4:258–267. [PubMed: 10859570]
- Garnier M, Henrich N, Dubois D. Influence of sound immersion and communicative interaction on the Lombard effect. *Journal of Speech, Language, and Hearing Research*. 2010; 53:588–608.
- Hotchkin CF, Parks SE. The Lombard effect and other noise induced vocal modifications: insight from mammalian communication systems. *Biological Reviews*. (In press).
- Jordan K, Weiss D, Hauser M, McMurray B. Antiphonal Responses to Loud Contact Calls Produced by *Saguinus oedipus*. *International Journal of Primatology*. 2004; 25:465–475.
- Lane H, Tranel B. The Lombard sign and the role of hearing in speech. *Journal of Speech, Language, and Hearing Research*. 1971; 14:677–709.
- Lesage V, Barrette C, Kingsley MCS, Sjare B. The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River estuary, Canada. *Marine Mammal Science*. 1999; 15:65–84.
- Love EK, Bee MA. An experimental test of noise-dependent voice amplitude regulation in Cope's grey treefrog, *Hyla chrysoscelis*. *Animal Behaviour*. 2010; 80:509–515. [PubMed: 20823939]
- Miksis-Olds JL, Tyack PL. Manatee (*Trichechus manatus*) vocalization usage in relation to environmental noise levels. *The Journal of the Acoustical Society of America*. 2009; 125:1806–1815. [PubMed: 19275337]
- Snowdon, CT.; Marc, N.; Klaus, Z.; Nicola, SC.; Vincent, MJ. *Advances in the Study of Behavior*. Academic Press; 2009. *Plasticity of Communication in Nonhuman Primates*; p. 239–276.
- Tressler J, Smotherman MS. Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats. *Journal of Comparative Physiology A*. 2009; 195:923–934.
- Weiss DJ, Garibaldi BT, Hauser MD. The production and perception of long calls by cotton-top tamarins (*Saguinus oedipus*): Acoustic analyses and playback experiments. *J Comp Psych*. 2001; 115:258–271.
- Weiss DJ, Hauser MD. Perception of harmonics in the combination long call of cottontop tamarins, *Saguinus oedipus*. *Animal Behaviour*. 2002; 64:415–426.

TABLE 1

Noise levels and treatment names for the six noise stimuli used in playback experiments. Each subject experienced all treatment types in random orders on separate days of testing. Noise playbacks were paired with same-day silent-playback trials (controls). All noise levels are given in dB re 20 μ Pa rms.

Noise level	Broadband (10 kHz)	Narrowband (5 kHz)
Loud	A (64.3 dB rms)	D (59.2 dB rms)
Medium	B (54.1 dB rms)	E (51.3 dB rms)
Quiet	C (46.7 dB rms)	F (44.1 dB rms)

TABLE 2

Summary of observed changes to acoustic structure of chirps and CLCs during increased noise. Call amplitude changes were more pronounced for CLCs than for chirps. Multiple frequency parameters for both call types also varied with changes in noise level.

Parameter	CLCs	Chirps
Amplitude	X	X
Duration		X
Frequency	X	X