RESEARCH ARTICLE

Noise-Induced Vocal Modulation in Cotton-Top Tamarins (*Saguinus oedipus*)

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The Lombard effect—an increase in vocalization amplitude in response to an increase in background noise—is observed in a wide variety of animals. We investigated this basic form of vocal control in the cotton-top tamarin (*Saguinus oedipus*) by measuring the amplitude of a contact call, the combination long call (CLC), while simultaneously varying the background noise level. All subjects showed a significant increase in call amplitude and syllable duration in response to an increase in background noise amplitude. Together with prior results, this study shows that tamarins have greater vocal control in the context of auditory feedback perturbation than previously suspected. Am. J. Primatol. 68:1183–1190, 2006. © 2006 Wiley-Liss, Inc.

INTRODUCTION

To successfully communicate with potential listeners, animals have developed a variety of strategies to overcome the masking effects of background noise, such as avoiding the noise by shifting the vocalization in time [Garcia-Rutledge & Narins, 2001], changing body posture during vocalization [Lengagne et al., 1999], and increasing the number [Lengagne et al., 1999; Potash, 1972b] or duration [Foote et al., 2004] of vocal elements (see Brumm and Slabbekoorn [2005] for a review). One of the most ubiquitous forms of noise compensation is an increase in vocalization amplitude. This basic effect, which was first described in humans by Lombard [1911], is found in a variety of vertebrates, including zebra finches [Cynx et al., 1998], nightingales [Brumm & Todt, 2002], Japanese quails [Potash, 1972a], cats [Nonaka et al., 1997], Beluga whales [Scheifele et al., 2005], macaques (*Macaca nemestrina* and *M. fascicularis* [Sinnott et al., 1975], and common marmosets [Brumm et al., 2004]. The effect has been documented for both vocalizations that are shaped by postnatal auditory experiences [Manabe et al., 1998] and those that are not [Potash, 1972a].

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Auditory-feedback-mediated vocal control is well established for both humans and songbirds [Doupe & Kuhl, 1999], while nonhuman primate vocal behavior is believed to be less dependent on auditory feedback [Janik & Slater, 2000]. However, studies of both Old World [Sinnott et al., 1975] and New World [Brumm et al., 2004] monkeys have shown robust Lombard effects, suggesting that at least some degree of auditory-feedback-mediated vocal control exists in nonhuman primates. The broad aim of this study was to extend the demonstration of the Lombard effect to another New World monkey, the cotton-top tamarin (*Saguinus oedipus*). More specifically, our goal was to build on prior results with this species [Miller et al., 2003; Egnor et al., 2006] by exploring the degree to which tamarins can control their vocal output in response to perturbations in auditory feedback. Our previous studies showed that tamarins can adjust the structure of their calls in the presence of brief perturbations to the acoustic environment. Here we examine the extent to which they can change the call structure in the presence of a continuous increase in background noise.

The cotton-top tamarin is a small New World monkey with a large (at least 38 distinct call types) and well-studied vocal repertoire [Cleveland & Snowdon, 1982]. We focused on a vocalization produced spontaneously following separation from the social group: the combination long call (CLC; see Fig. 1). The CLC is produced frequently and spontaneously in captivity by both males and females, and thus the production and perception of the CLC is an excellent system in which to explore the effects of environmental noise on vocal signal production. In addition, because one function of this call is to maintain contact with family group members [Cleveland & Snowdon, 1982], it is reasonable to assume that there has been strong selection on accurate transmission through the environment.
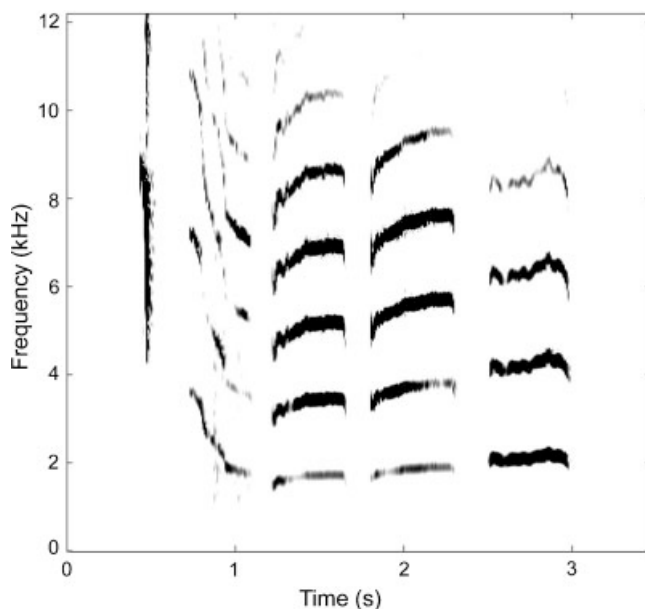

Fig. 1. Spectrogram of a cotton-top tamarin CLC. The CLC is produced spontaneously during social isolation. CLCs typically consist of one or two short frequency-modulated chirps followed by one or more longer whistles.

MATERIALS AND METHODS

Subjects

The subjects were three male and three female adult cotton-top tamarins from the Harvard University Cognitive Evolution Laboratory that ranged in age from 5 to 13 years. All of the subjects were born in captivity and socially housed, with separate home cages for each breeding pair and their offspring. The subjects were maintained on a diet of marmoset chow, sunflower seeds, peanuts, fruit, and yogurt. The animals were lured out of their home cages with a small piece of raisin, and they had ad libitum access to water.

Apparatus

Recordings were made in a double-walled sound-attenuating chamber (Industrial Acoustics, New York, NY; inner dimensions: $1.75\,m \times 1.85\,m \times 1.95\,m$) with a directional microphone (ME-66; Sennheiser, Old Lyme, CT) positioned $1\,m$ from the playback cage. The microphone signal was amplified (1202-VLZPro; Mackie, Woodinville, WA) and then digitized at a sampling rate of 24.4 kHz and a precision of 16-bit. Data acquisition and sound presentation were controlled with custom-built software (MATLAB; The Mathworks, Natick, MA) and an A/D,D/A board (RP2; Tucker-Davis Technologies, Alachua, FL). White noise playback (800–10,000 Hz) was generated in MATLAB, The Mathworks, Natick, MA, amplified (RA-100; Alesis, Cumberland, RI) and presented over a speaker (4'' mid-range; Radio Shack, Cambridge, MA). The subjects were monitored with a video camera during the recording sessions. The speaker was calibrated to be flat in amplitude (± 2 dB) from 800 Hz to 10 kHz at the beginning of every day using the following procedure: At the beginning of each session the microphone was placed in the playback cage at the approximate position of a subject's head. The impulse response of a system can be calculated by cross-correlating the input to the system $x(t)$ with the output of the system $y(t)$, provided that the autocorrelation of the input is a delta function. White noise is commonly used as $x(t)$. However, the autocorrelation of white noise is only a delta function for long (>30 seconds) durations, which is experimentally impractical. Golay codes [Golay, 1961] are short (~ 30 ms) complementary sequences with the property that, like long bursts of white noise, the sum of their autocorrelations is a delta function. Golay codes have been used in a variety of systems to estimate the impulse response of the acoustic environment, including studies of auditory feedback in animals [Foster, 1986; Leonardo, 2004; Zhou et al., 1992]. This measurement captures the impulse response of the D:A apparatus, speaker amplifier, speaker, room, and microphone. The background noise presented over the speaker was filtered with the inverse of this measured impulse response, which ensured that the spectrum of the white noise at the center of the playback cage was flat (± 2 dB) from 800 to 10,000 Hz over the range of amplitudes used in the study. Note that the microphone was measured to be flat ± 1.5 dB with a B&K microphone (4191) with a B&K preamplifier (2669B) and a B&K amplifying power supply (5935) (B&K, Norcross, GA), and was assumed to not contribute significantly to the measured impulse response. This calibration ensured that the noise amplitude was correct (either 50 or 70 dB SPL). To verify that the calibration was successful, the noise amplitude was also measured with a sound level meter (Radio Shack, Cambridge, MA).

To reduce changes in recorded amplitude due to changes in the direction the subject was facing, or the distance between the microphone and the subject, the

playback cage was made shallow and narrow (25 cm deep × 28 cm wide × 51 cm tall) with a wire mesh front and smooth opaque Plexiglas top, bottom, and sides. The tamarins spent the majority of their time perched on the wire mesh facing out, which ensured that they were facing the microphone while vocalizing.

Experimental Conditions

Individual subjects were placed in the recording chamber and continuous background noise was presented at either 50 ("Soft" condition) or 70 ("Loud" condition) dB SPL. Soft and Loud sessions were interleaved randomly for each individual subject. Sessions were continued until 11 calls were recorded from each subject in each noise condition. Noise levels were constant within a given recording session.

Denoising

The signal recorded on the microphone is the sum of the vocal response and the background noise presented over the speaker. In order to accurately characterize the amplitude of the vocalization, it is critical to remove the background noise. To do this we generated an accurate estimate of the noise alone by keeping a copy of the signal sent to the speaker and measuring the impulse response of the playback apparatus (the speaker, room, box, and microphone) using Golay codes as described above. We convolved the playback apparatus impulse response with the broadcast signal to produce an estimate of the noise signal on the microphone. This signal was then subtracted from the raw microphone signal, leaving a clean copy of the tamarin's vocalization.

Data Analysis

After denoising was performed the CLCs were cut out using an automated threshold algorithm and verified by hand. Calls were loaded into MATLAB and converted from voltage to pressure waveforms. We determined the total call dB SPL values by calculating the root mean square (RMS) of the signal and plugging it into the following function:

$$dB_{SPL} = 20 \cdot \log_{10}(RMS/p_0)$$

where p_0 is the standard reference pressure of 20 μPa. We calculated the magnitude of the Lombard effect by subtracting the average call amplitude in the Soft condition from that in the Loud condition. Syllable durations were measured from oscillograms plotted in MATLAB. Syllable fundamental frequencies were measured at the midpoint of the syllable from spectrograms (1,024-point fast Fourier transform, window width = 15 ms, overlap = 3 ms). The effects of noise amplitude on the call amplitude, syllable duration, syllable frequency, and syllable number were tested for significance with multifactorial analyses of variance (ANOVAs).

RESULTS

Methodological Results

Effect of noise amplitude on head orientation
To ensure that the direction in which the tamarin was facing (and therefore the amplitude recorded on the microphone) did not vary in a consistent way between the Loud and Soft conditions, we videotaped each recording session,

measured the direction of the tamarin's mouth at the midpoint of each CLC produced, and calculated the angle between that direction and an imaginary line running down the barrel of the microphone. We then calculated the average head orientation for each subject for both the Loud and Soft conditions. There was no consistent effect of background noise amplitude on average head orientation ($F_{1,5} = 2.27$, $P = 0.192$), which ensures that any amplitude differences observed are the result of true differences in call amplitude, rather than differences due to the directionality of the microphone or the sound radiation pattern of the calls.

Experimental Results

Call amplitude

CLC amplitude increased significantly in response to an increase in background noise ($F_{1,5} = 83.7$, $P = 0.0003$; Fig. 2). All of the subjects showed this effect, with magnitudes ranging from 7.1 to 12.5 dB.

Syllable number

The average syllable number was 3.8 for the soft condition and 3.6 for the loud condition (Table I). This difference was not significant ($F_{1,5} = 1.2$, $P = 0.323$).

Syllable duration

Average syllable duration increased significantly as a function of increase in background noise, from 410 to 505 ms ($F_{1,5} = 10.76$, $P = 0.02$; see Table I). All subjects showed this effect.

Syllable fundamental frequency

The average syllable fundamental frequency did not vary significantly as a function of background noise level ($F_{1,5} = 0.43$, $P = 0.54$; see Table I).
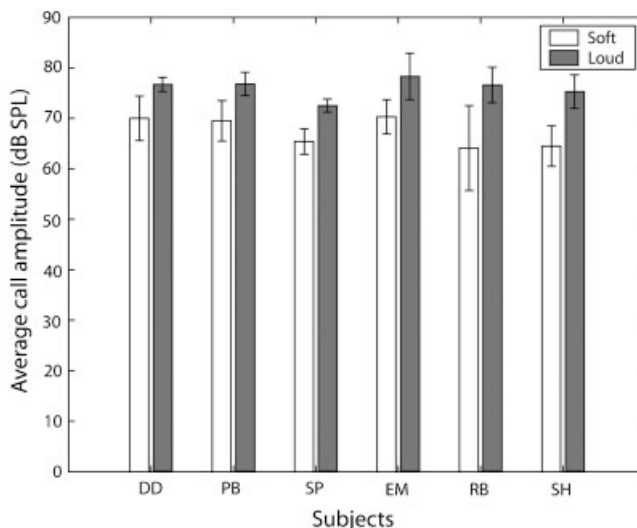

Fig. 2. Call amplitude in background noise. Cotton-top tamarins increase the amplitude of their vocalizations in the Loud condition (dark bars) relative to the Soft condition (white bars).

TABLE I. Syllable Number, Syllable Duration and Syllable Frequency[*]

Subject	Syllable duration (ms)		Number of syllables		Frequency (Hz)	
	Soft	Loud	Soft	Loud	Soft	Loud
DD	440 ± 30	500 ± 70	4.2 ± 0.4	4.5 ± 0.5	2350 ± 1080	1014 ± 1010
PB	360 ± 80	520 ± 10	3.9 ± 0.4	2.9 ± 0.5	2850 ± 2090	1674 ± 163
SP	340 ± 60	360 ± 70	4.1 ± 0.3	3.9 ± 0.4	3780 ± 2390	3460 ± 2253
EM	490 ± 40	690 ± 200	2.7 ± 0.5	2.6 ± 0.7	2540 ± 712	3110 ± 4226
RB	370 ± 30	460 ± 30	4.5 ± 0.4	4.2 ± 0.5	2220 ± 500	2070 ± 570
SH	460 ± 10	500 ± 70	3.4 ± 0.5	3.5 ± 0.5	1850 ± 400	1900 ± 510

[*]Average number of syllables per call, average syllable duration and average syllable frequency, plus or minus SD, in the soft and loud background noise conditions for each subject. Syllable duration increased as a function of background noise level, while syllable number and syllable frequency did not vary as a function of background noise level.

DISCUSSION

This study shows that cotton-top tamarins, a small New World monkey, can use auditory feedback to control the amplitude and duration of their species-specific contact call, the CLC. All subjects demonstrated the Lombard effect, i.e., they increased the amplitude of their vocalizations in response to an increase in background noise. In addition, the subjects also showed a significant increase in syllable duration. Although an increase in vocal amplitude is the most obvious and robust response to vocalizing in a noisy environment, other acoustic changes have also been observed in humans, including increases in the duration of utterances [reviewed in Brumm & Slabbekoorn, 2005; Lane & Tranel, 1971]. Interestingly, an increase in duration of vocal elements increases the intelligibility of speech [Picheny et al., 1986]. Cotton-top tamarins, therefore, respond to an increase in background noise level with adaptive changes in both the amplitude and duration of their vocal signals. This observation is consistent with a recent study in another Callitrichid, the common marmoset, which also demonstrated an increase in amplitude and syllable duration in response to an increase in background noise level [Brumm et al., 2004]. Duration increases have also been observed in humans with increased vocal effort [Traunmüller & Eriksson, 2000], and in baboons (*Papio hamadryas ursinus*) with increases in arousal intensity [Rendall, 2003].

In addition to duration changes, an increase in voice pitch has been consistently observed as an acoustic correlate of the Lombard effect in humans [e.g., Lombard, 1911; Van Summers et al., 1988; reviewed in Lane & Tranel, 1971]. This pitch increase is predicted as a biomechanical consequence of the increase in vocal amplitude [Lane & Tranel, 1971], and has also been shown to occur in Eastern towhees (*Pipilo erythrophthalamus*) [Nelson, 2000]. However, we observed no consistent change in syllable fundamental frequency as a function of background noise level. Further experiments will be necessary to determine whether this indicates that fundamental frequency is being actively stabilized, or whether the amplitude difference in the present experiment is simply too small to reveal a frequency difference.

Previous experiments in cotton-top tamarins that used brief sound bursts presented during the production of a CLC showed that changes in syllable number, interpulse-interval duration, and call amplitude occur when an

interfering acoustic event is locked to a vocal utterance [Miller et al., 2003; Egnor et al., 2006]. The current data demonstrate that amplitude and duration changes to call structure can also be induced by changes in continuous background noise level.

Vocal control exists in a variety of forms, including compensation for environmental masking, vocal accommodation, the acquisition of a local dialect, and vocal imitation. At present, little is known about the mechanisms underlying these different forms of auditory-feedback-mediated vocal control, or the extent to which these different forms are exhibited by nonhuman primates. Until such details are addressed, including the possibility that they are achieved in different organisms by different means, it will not be possible to account for phylogenetic patterns of convergence and divergence, or the opportunities for vocal plasticity that these mechanisms provide.

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