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Modification of spectral features by nonhuman primates

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Abstract

Ackermann et al. discuss the lack of evidence for vocal control in nonhuman primates. We suggest that nonhuman primates may be capable of achieving greater vocal control than previously supposed. In support of this assertion, we discuss new evidence that nonhuman primates are capable of modifying spectral features in their vocalizations.

In discussing the modulation of acoustic call structure, Ackermann et al. question the extent to which nonhuman primates exert operant control over the spectro-temporal features of their calls. This concern echoes a long-standing notion that nonhuman primates are capable of controlling acoustic parameters that can be modulated by changes in exhalation, such as loudness and duration, but lack control over spectral features that may require more nuanced control over the vocal apparatus (Janik & Slater 1997).

In this connection, we would like to briefly review our work on noise-induced vocal modifications in nonhuman primates. When vocalizing in noisy environments, humans and several other species (e.g., whales, bats, etc.; Hage et al. 2013; Parks et al. 2011; see review in Hotchkin & Parks 2013) involuntarily raise the amplitude of their vocalizations (i.e., the Lombard effect; Lombard 1911; Pick et al. 1989). Associated changes in vocalization duration have also been documented in humans and nonhumans (e.g., Garnier et al. 2010). Some species also modify spectral features by shifting energy to higher harmonics (reviewed in Hotchkin & Parks 2013). However, consistent with Ackermann et al.'s concerns, previous studies with nonhuman primates have suggested that they may be restricted to manipulating the amplitude and temporal aspects of their calls in response to noise in the transmission environment (Egnor & Hauser 2006; Sinnott et al. 1975). To the best of our knowledge, no nonhuman primate has previously demonstrated the ability to modify spectral features of their calls in response to noise.

We have recently discovered this ability in cotton-top tamarins (*Saguinus oedipus*), a small arboreal New World species known to have an extensive vocal repertoire (Cleveland & Snowdon 1982). A previous study with this species found that they modify the amplitude and duration of their calls in response to noise (Egnor & Hauser 2006), and, using a different method, we have determined they are also capable of modifying spectral components of their calls. Our findings suggest the possibility for greater vocal control in nonhuman primates than previously supposed (e.g., Janik & Slater 1997).

Unlike prior studies with nonhuman primates (Brumm et al. 2004; Egnor & Hauser 2006; Sinnott et al. 1975), our study used playbacks of both broad- and narrow-band white noise at a range of amplitudes to investigate vocal control of two call types, chirps and combination long calls (CLCs; Hotchkin 2012; Hotchkin et al. 2013). We measured a variety of acoustic parameters including spectral tilt (a relative measure of the distribution of energy between the high- and low-frequency components of the call), which is an acoustic parameter that has been studied almost exclusively in human responses to noise (e.g., Lu & Cooke 2009). We found that individuals modified the structure of both call types in response to changes in noise amplitude and bandwidth. In CLCs, whose frequencies were overlapped by the noise, peak fundamental frequency and spectral tilt changed in response to increased noise amplitude and bandwidth (see our Fig. 1). While the noise stimuli did not overlap with the chirp frequencies, this call type also showed changes to frequency content during noise. Noise with frequency components at or slightly below vocalization frequency may result in masking, due to a phenomenon known as the upward spread of masking which has been observed in both humans and nonhuman mammals (Egan & Hake 1950; Nachtigall et al. 2004). Increases in chirp frequency may provide release from masking by low-frequency noise, thereby improving the detectability even when noise frequencies do not overlap the vocalization. In chirps, the peak and maximum components of the fundamental frequency increased as a result of noise level, with no changes to spectral tilt. Other vocal modifications observed included the Lombard effect (i.e., an increase in amplitude) and longer chirp duration.

The focus of the authors is primarily on volitional control and modification of vocalizations in nonhuman primates, and they could therefore dismiss this finding because responses to noise are thought to reflect involuntary processes, as noted above. In fact, we do not argue that the flexibility exhibited in the Lombard effect and conditioning studies necessarily set the stage for the evolution of vocal flexibility as it is manifest in humans (as noted by Owren et al. 2011). However, in order to refine the dual stage hypothesis, it is important to fully describe the range of flexible features available in nonhuman primate vocal communication. Research with cotton-top tamarins alone has demonstrated they are capable of producing long-term changes to the acoustic structure of their calls (i.e., vocal convergence; see Weiss et al. 2001); perceiving changes to the spectral features of the harmonics in their CLCs (Weiss & Hauser 2002); modifying the timing of their calls (Egnor et al. 2007); and also altering the loudness, duration, and spectral components of their calls when transmitting signals in noisy environments (Egnor & Hauser 2006; Egnor et al. 2006; Hotchkin 2012). Further, it has been suggested that multiple levels of vocal control may be active during Lombard vocalizations and could involve a complex array of neural structures extending beyond brainstem reflexes (Eliades & Wang 2012). Thus, the main implication of our findings for the target article is to indicate that nonhuman primates may possess greater vocal control than has previously been supposed. Developing a more complete understanding of the ways in which nonhuman primates are capable of manipulating their vocalizations, and the supporting neural networks, may ultimately help Ackermann et al. further refine their theory.

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[The letters “a” and “r” before author’s initials stand for target article and response references, respectively]

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Figure 1.

(Weiss et al.). Representative CLCs produced during (a) control and (b) treatment trials demonstrating changes to spectral tilt. All whistles from (a) have strong fundamental frequencies and maximum energy in the 2nd harmonic, while in (b) the first whistle has a very faint fundamental frequency at approximately 2 kHz, and peak frequencies for all whistles occur in the 4th harmonics. Reduced energy in the fundamental frequency is also apparent in the second and third whistles. Spectrogram parameters: 1024 point Hamming window, 75% overlap, 11.7 Hz frequency resolution.