

RESEARCH ARTICLE

The Communicative Content of the Common Marmoset Phee Call During Antiphonal Calling

CORY T. MILLER^{1,2*}, KATHERINE MANDEL², AND XIAOQIN WANG²

¹Department of Psychology, Cortical Systems and Behavior Laboratory, University of California, San Diego, California

²Department of Biomedical Engineering, Laboratory of Auditory Neurophysiology, Johns Hopkins University, School of Medicine, Baltimore, Maryland

Vocalizations are a dominant means of communication for numerous species, including nonhuman primates. These acoustic signals are encoded with a rich array of information available to signal receivers that can be used to guide species-typical behaviors. In this study, we examined the communicative content of common marmoset phee calls, the species-typical long distance contact call, during antiphonal calling. This call type has a relatively stereotyped acoustic structure, consisting of a series of long tonal pulses. Analyses revealed that calls could be reliably classified based on the individual identity and social group of the caller. Our analyses did not, however, correctly classify phee calls recorded under different social contexts, although differences were evident along individual acoustic parameters. Further tests of antiphonal calling interactions showed that spontaneously produced phee calls differ from antiphonal phee calls in their peak and end frequency, which may be functionally significant. Overall, this study shows that the marmoset phee call has a rich communicative content encoded in its acoustic structure available to conspecifics during antiphonal calling exchanges. *Am. J. Primatol.* 72:974–980, 2010. © 2010 Wiley-Liss, Inc.

Key words: common marmoset; phee calls; antiphonal calling; dialects; information content

INTRODUCTION

Vocalizations are a central means of communicating information to conspecifics for most, if not all, vertebrate species. The significance of these signals in the evolutionary history of a species is reflected both in the complex array of information encoded within vocalizations and their functional role in mediating conspecific interactions. The common marmoset (*Callithrix jacchus*) produces a rich diversity of vocalizations [Bezera & Souto, 2008; Epple, 1968]. The most thoroughly studied of these vocal signals is the phee call, which has been the subject of several studies of acoustics, behavior, and neurobiology [Chen et al., 2009; Eliades & Wang, 2008; Jones et al., 1993; Miller & Wang, 2006; Miller et al., 2009a,b; Norcross & Newman, 1993, 1997; Norcross et al., 1994; Pistorio et al., 2006]. Detailed acoustic analyses of the marmoset phee call in adults revealed acoustic cues for the caller's individual identity [Jones et al., 1993] and gender [Norcross & Newman, 1993]. As these calls are primarily used for communicating with conspecifics occluded by vegetation or distance, other acoustic information may be encoded within the structure of this vocalization related to either the caller's identity or the behavioral context of the vocalization.

A critical vocal behavior exhibited by several species of nonhuman primates when visually occluded from conspecifics is antiphonal calling, a behavior involving the reciprocal exchange of species-specific contact calls between conspecifics [Biben, 1993; Miller et al., 2001a]. This vocal behavior in marmosets utilizes their species-typical phee call [Chen et al., 2009; Miller & Wang, 2006]. Our initial study showed that the timing of antiphonal calling exchanges changed because of the social relationship of the two animals engaged in the vocal interaction, suggesting that subjects recognize the caller's identity and relative relatedness [Miller & Wang, 2006]. Subsequent interactive playback experiments showed that the timing of the antiphonal call response is critical to maintaining the

Contract grant sponsor: NIH; Contract grant numbers: F32 DC007022; K99 DC009007; R01 DC005808.

*Correspondence to: Cory T. Miller, Department of Psychology, Cortical Systems and Behavior Laboratory, University of California, San Diego, 9500 Gilman Dr. #0109, La Jolla, CA 92093. E-mail: corymiller@ucsd.edu

Received 22 July 2009; revised 16 May 2010; revision accepted 16 May 2010

DOI 10.1002/ajp.20854

Published online 14 June 2010 in Wiley Online Library (wileyonlinelibrary.com).

behavior [Miller et al., 2009a], suggesting that, as in squirrel monkeys [Biben, 1993], social rules govern the temporal pattern of the antiphonal call sequences. In order for such interactions to occur, however, marmosets must be able to extract specific categorical information about other callers from the acoustic structure of the phee alone.

Building on earlier work, we sought to quantify the acoustic structure and communicative content of common marmoset phee calls during antiphonal calling. Identifying the various sources of acoustic variation in the call could provide insight into the types of information available to marmosets during antiphonal calling. We performed an acoustic analysis on a large corpus of phee calls to determine the various sources of communicative information available to conspecific signal receivers. Our analysis looks at three levels of information. First, we analyze the overall structure of the phee call to characterize its core spectro-temporal structure. Second, each vocalization communicates multiple levels of categorical information about the caller [Gerhardt, 1992; Miller & Cohen, 2010]. To examine the additional sources of acoustic information in the marmoset phee call, we used discriminant function analysis to test whether calls could be reliably classified based on the caller's individual identity, gender, and group membership. Third, we tested whether changes in behavioral context affect the structure of phee calls. As the phees in this study were recorded during antiphonal calling exchanges between animals that varied in their social relationship, we analyzed whether consistent acoustic differences were evident in the call structure in these social scenarios.

METHODS

Subjects

We recorded 1,313 phee calls produced by eight adult common marmosets (four male and four female) housed at Johns Hopkins University (Baltimore, MD). The common marmoset is a small-bodied (~400 g), New World primate endemic to the rainforests of northeastern Brazil [Bezera & Souto, 2008; Rylands, 1993]. Subjects comprised the pair-bonded breeding pairs of four different social groups. These social groups consisted of their pair-bonded breeding pair and up to two generations of offspring. These groups had all been together for a minimum of 1 year before testing. Animals are given ad libitum access to water and fed a diet consisting primarily of monkey chow and supplemented with other items, such as fruit, nuts, and yogurt. All experimental protocols were approved by the Johns Hopkins University Animal Use and Care Committee and complied with the American Society of Primatologists' Principles for the Ethical Treatment of Non Human Primates.

Acoustic Recording Procedure

We transported subjects from the colony to the testing room in transport cages. During transportation, we prevented any visual recognition of the other individual in the experiment by ensuring that subjects were visually occluded from each other at all times. The testing room was 7 m × 4 m in size and had the walls covered completely in acoustic attenuating foam and a carpet floor. This testing room is situated a far distance from the colony room. Animals in the testing room could not hear any vocalizations produced by animals in the colony room. Once inside the room, we placed subjects in wire mesh cages—each animal in an individual cage—separated by 2 m with an opaque cloth occluder equidistant between the two cages. Animals could interact vocally, but could not obtain visual cues from each other during the length of the experiment. We aimed a directional microphone (Sennheiser ME-66: frequency response 50–20,000 Hz) at each cage and recorded (44.1 kHz sampling rate) all vocalizations produced by subjects directly to the hard drive either on an Apple G4 powerbook or on G5 Desktop computer using a Digidesign Mbox I/O device and Raven Bioacoustics Software (Cornell, Lab of Ornithology). Each test session lasted for 15 min. After an experiment, we returned subjects to their home cage and cleaned the cages in the test room.

Behavioral Contexts

The vocalizations of all the subjects were recorded in four different behavioral contexts. Three of these conditions consisted of pairing animals with individuals of different social relationships: cagemate (CM), non-cagemate of the same gender (NCM-SS), and non-cagemate of the opposite gender (NCM-OS). For the fourth condition, the vocalizations produced by an isolated single animal in the test cage were recorded (ALONE). Subjects participated in each condition three times in randomized order. In the CM condition, subjects were always paired with their mate. For all behavioral conditions, we distinguished between phee calls produced as antiphonal and spontaneous calls. After our earlier work [Miller & Wang, 2006; Miller et al., 2009a], we considered a vocalization of an antiphonal call if the marmoset produced a phee call within 10 s of the other subject producing a phee call. All other phees were classified as spontaneous calls.

Acoustic Analysis

Phee calls were digitized as individual files for analysis. Using custom Matlab (Mathworks, Inc, Natick, MA) code written by CTM, we analyzed the following spectro-temporal features for each phee call: call duration (s), inter-pulse interval (s), pulse

duration (s), duration from phee onset to peak frequency (s), duration from peak frequency to phee offset (s), pulse start frequency (Hz), pulse end frequency (Hz), pulse mean frequency (Hz), pulse minimum frequency (Hz), pulse peak frequency (Hz), pulse delta frequency (Hz), slope 1: slope from phee onset to peak frequency (Hz/s), and slope 2: slope from peak frequency to phee offset (Hz/s). The Matlab code used for this analysis was semi-automated. For each call, a spectrogram was generated and the onset and offsets of each pulse marked manually. The F0 contour was then extracted automatically from between these time events.

Statistical Analyses

All statistical analyses were performed using SPSS, Chicago, IL (v16.0). The data presented for the “core acoustic structure” section are descriptive and, as such, have no statistical tests. Analyses of the “information content” and differences in phee calls between “social contexts” primarily used discriminant function analyses (DFA). This test uses a multi-dimensional space of independent variables for predicting group membership to a specific categorical-dependent variable. We utilized discriminant functions to test whether a model could be generated to correctly classify the “information content” and “social context” of phee calls based on the set of acoustic features. For cross-validation, half of the data set for a particular test was chosen at random and used to build the function and then the second half of the data set was then run through the original function to test how accurately these new data were classified. As the same data set was used in each of the three DFA tests, we used a Bonferroni corrected α level of $P < 0.01$. We followed this analysis up with a nested permutation test in which the identity of the caller was nested in the analysis for the main effect of the gender and group identity of the caller. This analysis also determines the extent to which a category can be classified, but is considered a more conservative estimate as it accounts for variability that is specific to individual differences. To examine whether individual acoustic features were distinguishable along these experimental categories, we used multivariate multiple regression analysis. As this latter analysis involved 24 different variables that were repeatedly tested, a Bonferroni corrected significance level was used: $P < 0.002$ (two-tailed).

RESULTS

Core Acoustic Structure

We recorded 1,313 phee calls from eight adult common marmosets. The number of calls recorded from each individual were as follows: female-1: 84; female-2: 214; female-3: 275; female-4: 90; male-1: 81; male-2: 271; male-3: 140; male-4: 158. The

majority of these calls ($n = 865$) consisted of two pulses (Fig. 1A). The number of two pulse phee calls recorded from each individual were as follows: female 1: 46; female 2: 173; female 3: 212; female 4: 82; male 1: 40; male 2: 129; male 3: 78; male 4: 105. As the most typical phee calls consists of two pulses, our analyses focused on calls with this structure. We observed no difference in the number of pulses produced between any of the measures tested here (i.e. information content or social context). Figure 1 plots the mean (SD) for the temporal (Fig. 1B) and spectral (Fig. 1C) features measured in our analysis. Overall, the phee call is a tonal vocalization consisting of a series of relatively long duration, gradually frequency modulating pulses. Each pulse increases in frequency over its length followed by a rapid drop in frequency within ~ 200 – 300 ms of pulse cessation (Fig. 1A). Both pulses have similar durations, though the first pulse (“p1”) generally exhibits a smaller change in frequency (mean = 1,558.9 Hz, SD = 27.04) than the second pulse (“p2”) (mean = 2,426.7 Hz, SD = 42.1). The second pulse in the phee call also typically has a higher mean and peak frequency, as well as a greater frequency bandwidth (Fig. 1C). The differences in duration and frequency modulation are also reflected in the slopes of the two pulses. Data show that the second pulse of the marmoset phee call has a sharper onset and offset slope relative to the first pulse (Fig. 2).

Information Content

We performed a series of DFA to test whether phee calls could be correctly classified into distinct categories based on the acoustic structure. The first analysis tested the individual identity of the caller. The discriminant function performed in this study was able to correctly classify the individual caller 92.0% of the time, whereas a cross-validation test correctly classified the caller 90.5% (Fig. 3). The first two functions were able to account for 82% of the variance ($F1$: eigenvalue = 10.25, Wilks' λ : $P < 0.0001$; $F2$: eigenvalue = 8.68, Wilks' λ : $P < 0.0001$) suggesting that acoustic structure of the marmoset phee call during antiphonal calling is idiosyncratic for each caller.

Overall, the following acoustic features were significantly different between male and female phee calls: call duration, pulse duration (p1&2), duration to peak frequency (p1&2), duration from peak frequency to pulse end (p1&2), start frequency (p2) end frequency (p1&2), mean frequency (p2), minimum frequency (p2), peak frequency (p2), delta frequency (p2), slope 1 (p1&2), and slope 2 (p1&2). Discriminant functions performed in this study were able to correctly classify the call as being produced by either a male or female 92.5% of the time, whereas the cross-validation test had a 91.9% correct classification. The function was able to account for 99% of the variance (eigenvalue: 1.863, Wilks' λ : $P < 0.0001$).

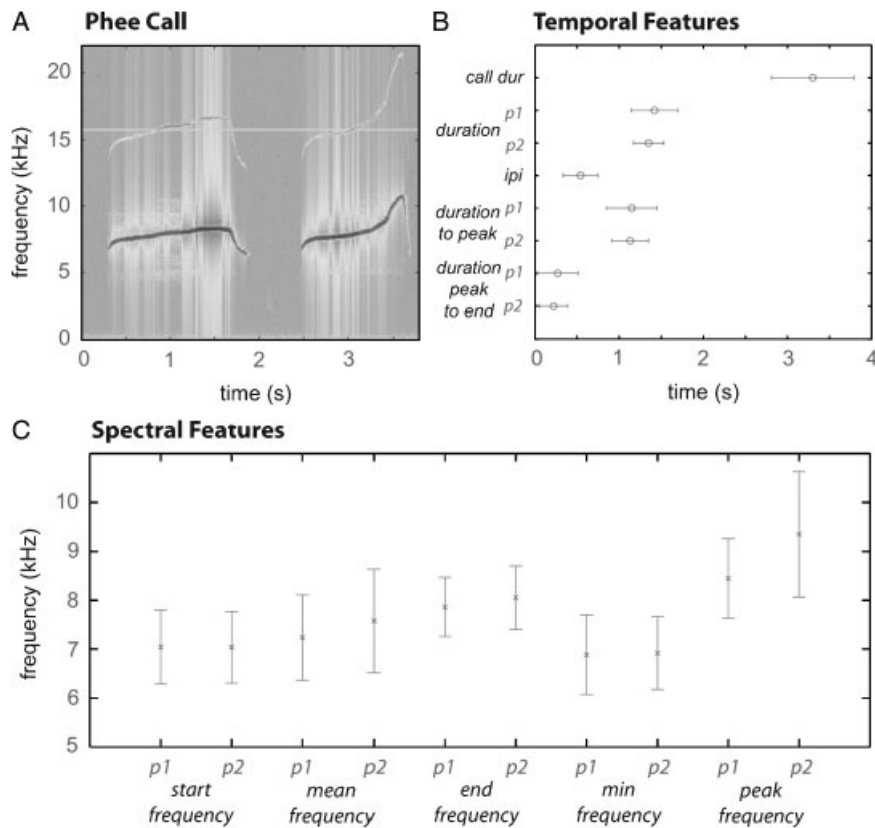


Fig. 1. Spectro-temporal structure of marmoset phee calls. (A) A spectrogram of a phee call. (B) Temporal features measured for all phee calls. Features measured in both the first and second pulses of the phee are noted by “p1” (pulse 1) and “p2” (pulse 2). The mean of each feature is noted with a “o,” error bars mark standard deviation. (C) Spectral features measured for all phee calls. Features measured in both the first and second pulses of the phee are noted by “p1” (pulse 1) and “p2” (pulse 2). The mean of each feature is noted with a “*,” error bars mark standard deviation.

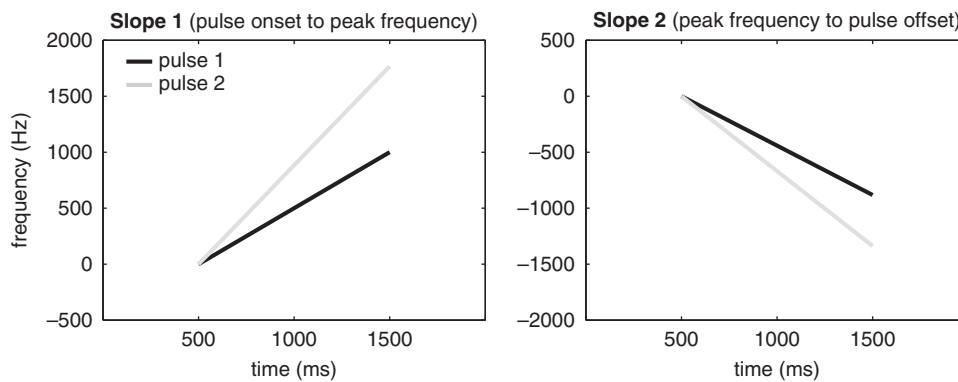


Fig. 2. Slopes for phee calls. Slope 1, shown to the left, plots the rising slope (Hz/s) in phee calls that occurs from the pulse onset to the peak frequency. Slope 2, shown to the right, plots the descending slope (Hz/s) from the peak frequency to the pulse onset. Pulse 1 is shown in the black line, whereas pulse 2 is shown in the gray line.

The more conservative nested permutation test, however, was not able to significantly classify the call as being produced by either a male or female. This analysis correctly classified the gender of the caller only 22% of the time, with a cross-validation test of 31% correct classification.

To test whether common marmoset phee calls showed evidence of group signatures in the acoustic

structure of phee calls, we performed a discriminant function using the original social group of subjects as the classifier. The eight animals used in this analysis were the pair-bonded adult animals in four different social groups. The analysis was able to correctly classify 87.1% of the phee calls to the appropriate social group, whereas the cross-validation test classified 85.4% of the calls correctly. The first

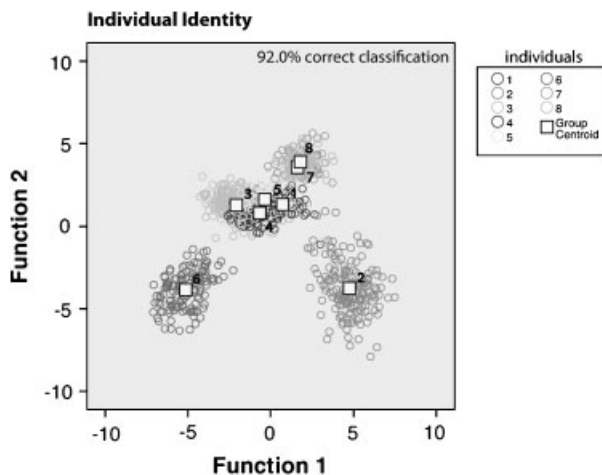


Fig. 3. Discriminant functions for caller identity information. Plots the first and second functions from the discriminant function analysis for “individual identity.” Squares mark the group centroids for each of the eight individuals whose calls were analyzed in the study, whereas colored open circles depict individual vocalizations produced by each individual.

function alone was able to account for 84% of the variation (eigenvalue: 5.49, wilks' λ : $P < 0.0001$). The more conservative nested permutation test, however, was able to classify calls as being produced by a particular social group 60% of the time. The cross-validation test was able to correctly classify calls in this analysis 53% of the time. Both are notably higher than the 25% correct classification that would be expected by chance.

Equal N Analysis

Given the variability in the number of phee calls contributed by each individual, we performed the same analysis with an equal sample of vocalizations for each marmoset ($n = 40$). Overall, the results were comparable to the above analyses using all the recorded phee calls. A DFA performed to test for individual identity in phee call structure was able to correctly classify the calls to the individual caller 97.5% of the time, whereas the cross-validation test correctly classified 93.1% of phees to the caller. The DFA performed to test for sex differences in phee calls correctly classified phees as either male or female 91.6% of the time and 90.3% in the cross-validation test. The final DFA tested for group signatures in the phee calls. This analysis correctly classified phees as belonging to one of the four groups for 91.3% of the vocalizations. The cross-validation test also performed well, correctly classifying 88.1% of the calls.

Social Context

During recording sessions, subjects were placed in the testing room either alone (ALO) or with a second conspecific in a visually occluded separate test

cell. These paired recordings occurred with conspecifics that varied in social context. Specifically, the pair of subjects was either CM, NCM-SS or NCM-OS. A discriminant function, however, was only able to classify 42.8% of the phees to the correct social context. Although this degree of classification is slightly above chance (25%), it does suggest considerable overlap in the acoustic structure of the phee call across these four social contexts. Thirteen individual acoustic features were significantly different across the contexts, though no consistent pattern was evident.

With the exception of the ALO context, subjects produced both spontaneous and antiphonal calls during these recording sessions. A discriminant function was able to correctly classify the calls as antiphonal or spontaneous only at chance (59.0%) suggesting that the global acoustic differences may not be consistent enough to determine their context. Two acoustic features, however, were significantly different between antiphonal and spontaneous calls. Both the end frequency ($P < 0.0001$) and peak frequency ($P = 0.002$) were significantly higher in the second pulse of spontaneously produced phee calls. Although the general structure of the phee call in these two contexts may be quite similar, particular features may signal whether the call was produced either spontaneously or as an antiphonal response.

DISCUSSION

Vocalizations convey an assemblage of information. The aim of this study was to build on earlier work [Miller et al., 2009a; Miller & Wang, 2006] and to quantify the relationship between the acoustic structure of the marmoset phee call and the communicative content of the signal during antiphonal calling by correlating the changes in its spectro-temporal features with behaviorally meaningful levels of information. Clearly more detailed perceptual studies are needed to determine the extent to which the animals themselves attend to the different sources of communicative content in the signal [Fischer et al., 2001; Gerhardt, 1991; Ghazanfar et al., 2002; Miller & Hauser, 2004; Miller et al., 2005; Nelson & Marler, 1989; Nowicki et al., 2001], but a detailed quantitative analyses of signal structure and any contextual changes that occur are necessary to guide these studies.

The phee call has a relatively stable, stereotyped acoustic structure (Fig. 1) and is encoded with a rich array of categorical acoustic information available to conspecific signal receivers during antiphonal calling exchanges. Consistent with earlier work [Jones et al., 1993; Norcross & Newman, 1993], DFA showed that phee calls produced during antiphonal calling exchanges contain acoustic signatures for the individual identity (Fig. 3) of the caller. Like an earlier study of the cotton-top tamarin (*Saguinus oedipus*)

[Weiss et al., 2001], a closely related *Callitrichid* species, the same analysis showed evidence of sex-specific signatures in the marmoset phee call. A more conservative permutation test, however, did not find the same type of classification suggesting that individual differences may underlie these other acoustic categories. This is somewhat surprising given that several studies of primates [Rendall et al., 2004], including cotton-top tamarins [Miller et al., 2004], found that individuals readily discriminated between the calls of males and females. More work is needed to resolve this issue and to determine the relationship between the acoustic features of marmoset calls and how reliably the sex of a caller can be recognized by the conspecifics. Following in the tradition of earlier work in tamarins [Miller et al., 2001b; Miller et al., 2004; Weiss et al., 2001], future studies of the marmoset phee call will aim to perceptually test the functional salience and significance of the categorical information encoded in the acoustic structure of this vocalization.

The presence of consistent acoustic differences between individuals of different social groups indicates the presence of cage signatures in this colony. For such acoustic signatures to develop, animals must possess the necessary mechanisms for sensory-feedback and vocal control to modify their vocalizations by matching the acoustic properties of animals within the social group. Previous studies of other *Callitrichid* species showed similar evidence [Snowdon & Elowsen, 1999; Weiss et al., 2001]. These cage signatures are particularly interesting because all animals within the colony are able to hear the vocalizations of all the other animals. Common marmosets' ability to develop signatures under captive conditions may be related to the regional dialects reported in wild populations of pygmy marmosets (*Cebuella pygmaea*) [De la Torre & Snowdon, 2009]. One possible explanation for the extensive evidence of group signatures and dialects in *Callitrichid* species may relate to their strong territoriality [Garber et al., 1993; Lazaro-Perea, 2001]. In addition to physical territorial markers, vocalizations may provide a further means of making an in-group/out-group distinction. Although historically many believed nonhuman primates possessed little or no control over their vocalizations [Egnor & Hauser, 2004], recent evidence suggests a more sophisticated system of vocal control in this taxonomic group [Egnor et al., 2006, 2007; Miller et al., 2003; Miller et al., 2009b; Suguira, 1998]. *Callitrichids*, in particular, appear to possess one of the most extensive systems of vocal control in primates.

The common marmoset phee call is rich with communicative information. Despite its stereotyped structure, subtle changes in spectro-temporal features yield at least three stable sources about the caller: individual identity, gender, and social group.

In summary, this study shows that common marmosets are provided with a diverse array of information when hearing a phee call during antiphonal calling. The extent to which this information is perceived and used by receivers, however, is not known. Future studies will build on this result to experimentally test the perceptual and social significance of the acoustic information available in the phee call during antiphonal calling at both the behavioral and neural levels.

ACKNOWLEDGMENTS

We thank Yi Zhou for her helpful comments on this manuscript and Roger Mundry for his generous help performing the permutation test analyses. This work was supported by grants from the NIH to CTM (F32 DC007022, K99 DC009007) and XW (R01 DC005808). All experimental protocols were approved by the Johns Hopkins University Animal Use and Care Committee and complied with the American Society of Primatologists' Principles for the Ethical Treatment of Non Human Primates (www.asp.org/society/resolutions/EthicalTreatmentofNonHumanPrimates.html).

LITERATURE CITED

- Bezera BM, Souto A. 2008. Structure and usage of the vocal repertoire of *Callithrix jacchus*. *International Journal of Primatology* 29:671–701.
- Biben M. 1993. Recognition of order effects in squirrel monkey antiphonal call sequences. *American Journal of Primatology* 29:109–124.
- Chen HC, Kaplan G, Rogers LJ. 2009. Contact calls of common marmosets (*Callithrix jacchus*): influence of age of caller on antiphonal calling and other vocal responses. *American Journal of Primatology* 71:165–170.
- De la Torre S, Snowdon CT. 2009. Dialects in pygmy marmosets? Population variation in call structure. *American Journal of Primatology* 71:1–10.
- Egnor SER, Hauser MD. 2004. A paradox in the evolution of primate vocal learning. *Trends in Neurosciences* 27:649–654.
- Egnor SER, Iguina C, Hauser MD. 2006. Perturbation of auditory feedback causes systematic perturbation in vocal structure in adult cotton-top tamarins. *Journal of Experimental Biology* 209:3652–3663.
- Egnor SER, Wickelgren JG, Hauser MD. 2007. Tracking silence: adjusting vocal production to avoid acoustic interference. *Journal of Comparative Physiology A* 193:477–483.
- Eliades SJ, Wang X. 2008. Neural substrates of vocalization feedback monitoring in primate auditory cortex. *Nature* 453:1102–1106.
- Epple G. 1968. Comparative studies on vocalizations in marmoset monkeys. *Folia Primatologica* 8:1–40.
- Fischer J, Metz M, Cheney DL, Seyfarth RM. 2001. Baboon responses to graded bark variants. *Animal Behaviour* 61:925–931.
- Garber PA, Pruettz JD, Isaacson J. 1993. Patterns of range use, range defense and intergroup spacing in moustached tamarin monkeys (*Saguinus mystax*). *Primates* 34:11–25.
- Gerhardt HC. 1991. Female mate choice in treefrogs: static and dynamic acoustic criteria. *Animal Behaviour* 42:615–636.

- Gerhardt HC. 1992. Multiple messages in acoustic signals. *Seminars in the Neurosciences* 4:391–400.
- Ghazanfar AA, Smith-Rohrberg D, Pollen A, Hauser MD. 2002. Temporal cues in the antiphonal calling behaviour of cotton-top tamarins. *Animal Behaviour* 64:427–438.
- Jones BA, Harris DHR, Catchpole CK. 1993. The stability of the vocal signature in phee calls of the common marmoset, *Callithrix jacchus*. *American Journal of Primatology* 31:67–75.
- Lazaro-Perea C. 2001. Intergroup interactions in wild common marmosets, *Callithrix jacchus*: territorial defence and assessment of neighbours. *Animal Behaviour* 62:11–21.
- Miller CT, Beck K, Meade B, Wang X. 2009a. Antiphonal call timing in marmosets is behaviorally significant: interactive playback experiments. *Journal of Comparative Physiology A* 195:783–789.
- Miller CT, Eliades SJ, Wang X. 2009b. Motor-planning for vocal production in common marmosets. *Animal Behaviour* 78:1195–1203.
- Miller CT, Cohen YE. 2010. Vocalizations as auditory objects: behavior and neurophysiology. In: Platt M, Ghazanfar AA, editors. *Primate neuroethology*. New York, NY: Oxford University Press. p 237–255.
- Miller CT, Dibble E, Hauser MD. 2001a. Amodal completion of acoustic signals by a nonhuman primate. *Nature Neuroscience* 4:783–784.
- Miller CT, Miller J, Costa RGD, Hauser MD. 2001b. Selective phonotaxis by cotton-top tamarins (*Saguinus oedipus*). *Behaviour* 138:811–826.
- Miller CT, Flusberg S, Hauser MD. 2003. Interruptibility of cotton-top tamarin long calls: implications for vocal control. *Journal of Experimental Biology* 206:2629–2639.
- Miller CT, Hauser MD. 2004. Multiple acoustic features underlie vocal signal recognition in tamarins: antiphonal calling experiments. *Journal of Comparative Physiology A* 190:7–19.
- Miller CT, Iguina C, Hauser MD. 2005. Processing vocal signals for recognition during antiphonal calling. *Animal Behaviour* 69:1387–1398.
- Miller CT, Scarl JS, Hauser MD. 2004. Sensory biases underlie sex differences in tamarin long call structure. *Animal Behaviour* 68:713–720.
- Miller CT, Wang X. 2006. Sensory-motor interactions modulate a primate vocal behavior: antiphonal calling in common marmosets. *Journal of Comparative Physiology A* 192:27–38.
- Nelson DA, Marler P. 1989. Categorical perception of a natural stimulus continuum: Birdsong. *Science* 244:976–978.
- Norcross JL, Newman JD. 1993. Context and gender specific differences in the acoustic structure of common marmoset (*Callithrix jacchus*) phee calls. *American Journal of Primatology* 30:37–54.
- Norcross JL, Newman JD. 1997. Social context affects phee call production by nonreproductive common marmosets (*Callithrix jacchus*). *American Journal of Primatology* 43:135–146.
- Norcross JL, Newman JD, Fitch WT. 1994. Responses to natural and synthetic phee calls by common marmosets. *American Journal of Primatology* 33:15–29.
- Nowicki S, Searcy WA, Hughes M, Podos J. 2001. The evolution of bird song: male and female response to song innovation in swamp sparrows. *Animal Behaviour* 135:615–628.
- Pistorio A, Vintch B, Wang X. 2006. Acoustic analyses of vocal development in a New World primate, the common marmoset (*Callithrix jacchus*). *Journal of the Acoustical Society of America* 120:1655–1670.
- Rendall D, Owren MJ, Weerts E, Hienz RD. 2004. Sex differences in the acoustic structure of vowel-like vocalizations in baboons and their perceptual discrimination by baboon listeners. *Journal of the Acoustical Society of America* 115:411–421.
- Rylands AB. 1993. *Marmosets and tamarins: systematics, behaviour, and ecology*. Oxford, UK: Oxford University Press.
- Snowdon CT, Elowson AM. 1999. Pygmy marmosets modify call structure when paired. *Ethology* 105:893–908.
- Sugira H. 1998. Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. *Animal Behaviour* 55:673–687.
- Weiss DJ, Garibaldi BT, Hauser MD. 2001. The production and perception of long calls by cotton-top tamarins (*Saguinus oedipus*): acoustic analyses and playback experiments. *Journal of Comparative Psychology* 11:258–271.