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Antiphonal Responses to Loud Contact Calls Produced by *Saguinus oedipus*

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*We report the results of an experiment designed to investigate whether captive cotton-top tamarins (*Saguinus oedipus*) selectively call back to an absent cagemate. We removed 2 individuals living in separate cages (cycling through the colony so that each individual was removed 10 times) from the homeroom and played back calls produced by one of them. The caller's cagemate, residing in the homeroom, was more likely to be the first individual to call back antiphonally than any other individual in the colony was. In support of previous work using both habituation-discrimination and phonotaxic techniques, our results show that cotton-top tamarins can recognize cagemates and possibly individuals by voice alone, and that the antiphonal playback method provides yet another tool for investigating acoustic perception in nonhuman primates.*

KEY WORDS: acoustic perception; antiphonal calling; cotton-top tamarin; vocal signatures.

INTRODUCTION

Communication involving long-distance signaling occurrs within a network, in which all signalers and perceivers in range of each other can potentially interact (McGregor and Dabelsteen, 1996). Antiphonal calling represents a form of interactive communication and occurs in a wide variety of species, including insects, frogs, birds, and primates. Many field studies of antiphonal vocal interactions among primates have been focused on the production of long or loud call bouts (Mitani and Stuht, 1998; Waser,

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1982). These high intensity, stereotyped calls are typically produced in the context of isolation, and often elicit similar vocalizations from conspecifics. Consequently, they may serve as location signals for conspecifics, providing information about caller identity, sex, and group membership.

Cotton-top tamarins produce several types of long calls, often during physical separation from other group members (Cleveland and Snowdon, 1982). The combination long call (CLC), consisting of 2-3 initial chirps followed by 2-5 whistles, is one variant. Snowdon *et al.* (1983) found evidence for group discrimination through laboratory playback tests using two types of long calls (normal and quiet). Weiss *et al.* (2001) analyzed CLCs from a colony of adult cotton-top tamarins and found that they could be accurately assigned to the appropriate individual, sex, and cage-group. Habituation-discrimination playbacks using both natural and synthetic stimuli showed that individuals could be recognized by voice alone (Weiss & Hauser, 2002). The procedure entails habituating a subject to one set or class of stimuli, e.g., a variety of CLCs from one individual, followed by the playback of a test stimulus from another set or class, e.g., a CLC from another individual. If the subject responds to the test stimulus following habituation, it provides evidence that the subject considered the change between sets to be meaningful.

When studying any communicative signals, one must consider that the social relationship between sender and receiver plays a critical role in the kinds of responses that can be elicited, given that the acoustic signal alone is not the only source of information. Instead, all acoustic signals are fundamentally embedded within a social and ecological context (West and King, 1996; Rendall *et al.*, 1999; Owings and Morton, 1998). As communication often involves >2 individuals, different organisms will hear the same signal. All receivers may have the ability to discriminate between signalers but may respond to the signal in different ways. This, in turn, will affect the signaler, which will affect the signaler's next utterance, and so on. Therefore, a complete understanding of vocal communication also necessitates an understanding of this interactive, social context of communication, but few studies of nonhuman primate vocal communication have taken this context into account (McGregor and Dabelsteen, 1996; Harcourt *et al.*, 1993).

CLCs are typically produced by isolated individuals, often eliciting responses by other group members (Cleveland and Snowdon, 1982). Studies using isolated subjects and the habituation-discrimination procedure cannot provide a complete understanding of the communicative function of CLCs. For example, despite previous research that has shown that individual identity is encoded in the CLC (Weiss *et al.*, 2001), we do not know whether particular individuals within a group may be more or less sensitive to the differences, nor do we know which individuals within the group produce antiphonal CLCs. We attempted to further our understanding of the variables mediating the antiphonal calling behavior in *Saguinus oedipus*. Specifically, our goal was to explore whether tamarins respond differentially to CLCs from other group members. We investigated whether the ability to discriminate between individuals (evidenced in isolation; Weiss *et al.*, 2001) generalizes to a different context using a new behavioral assay: antiphonal calling by group members to calls produced by lone individuals visually isolated from the group.

METHODS

Subjects

There were 6 cagegroups of tamarins throughout the experiment (Table I). The colony comprised 19 captive-born cotton-top tamarins: 13 adults, 2 juveniles, and 4 infants. We used 11 of the 13 adults as subjects. At the onset of the experiment, there were 5 cages of mated pairs (one with an adult female offspring, which, like the younger offspring, was not used as a subject) and one cage of a mated pair, their 2 adolescents, and 2 infants. By the end of the experiment, the colony consisted of 3 cages of family groups with infants and 3 cages of mated pairs without offspring (Figure 1).

The tamarins' cages (1.8 × 1.5 × .8 m) were stainless steel and Plexiglas and had tree branches, wooden perches and nest boxes inside. The tamarin

Table I. Individuals in the tamarin colony

Tamarin identity	Sex	Cage group number	Date of birth	Used as subject?
RW	M	1	1994	Y
SH	F	1	1995	Y
ID	M	2	1994	Y
EM	F	2	1992	Y
PB	M	2	1999	N
KW	F	2	1999	N
FK	M	2	2000	N
NK	F	2	2000	N
DD	M	3	1991	Y
ES	F	3	1991	Y
RB	F	3	1996	N
RJ	M	4	1997	N
UB	F	4	1987	Y
PJ	M	4	2000	N
AC	M	5	1993	Y
JG	F	5	1995	Y
JM	M	5	2000	N
SP	M	6	1992	Y
EN	F	6	1995	Y

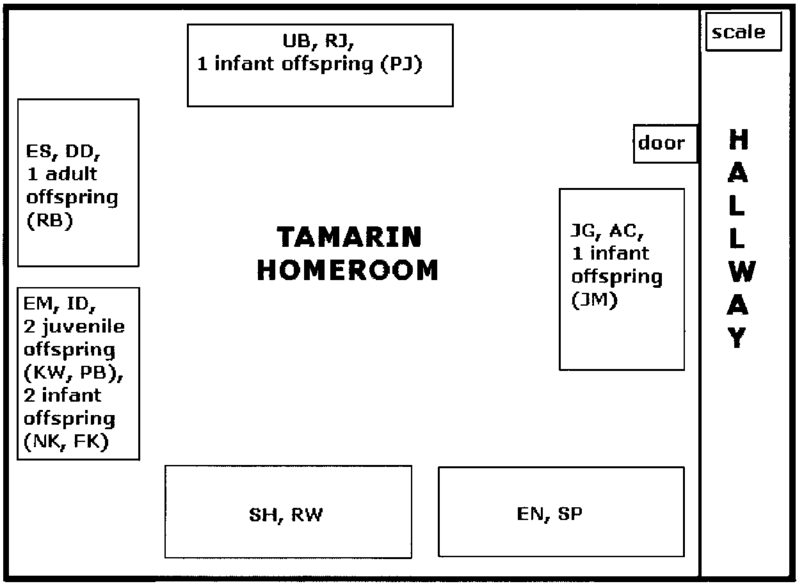

Fig. 1. The tamarin colony homeroom set-up. At the beginning of the experiment, the 2 cages nearest the door contained no offspring. The only change over the course of the experiment was the birth of 2 infants, which are included in the figure. Also pictured is the hallway scale where the tamarins are weighed daily.

diet consisted of Purina chow, crickets, mealworms, fruit, sunflower seeds, and supplemental vitamins provided once a day after the experiments; the diet was supplemented by food received during various laboratory experiments. Water was provided ad libitum, and all groups were on a 12L:12D light cycle.

Stimuli

We recorded CLC stimuli from individual tamarins either when alone in an acoustically isolated chamber (Industrial Acoustics Co., Inc., Model 400-A) or in an isolate condition of a previous experiment on social communication. During all sessions, we placed tamarins in a wire test cage (45 × 45 × 20 cm). We recorded calls on a Tascam DAT via a Sennheiser ME-60 microphone. In the isolate condition of the social communication experiment, we transported subjects into a test room that was likewise visually and acoustically isolated from the colony's homeroom. We placed the subjects in an apparatus consisting of 2 runways separated by a Plexiglas barrier. We recorded calls (Tascam DAT, Sennheiser ME66) only when the subject was alone in this apparatus.

All vocalizations were acquired (48 kHz sample rate) with Sound Designer II and an Audiomedia II sound card. We hi-pass filtered all calls obtained below the fundamental frequency (as determined by a 1024 point FFT spectrogram). We then normalized the amplitude of calls with respect to their peak amplitudes because recording distances were not always the same across and within subjects. We selected calls randomly from a set of high-quality recordings to ensure that they were representative of the natural variation within individuals.

To avoid problems of pseudoreplication, we presented 5 different calls per individual. Some call sets included exemplars recorded in different apparati, though in similar conditions. An acoustic analysis of the calls showed no significant difference between the call sets (Weiss *et al.*, 2001). In addition, previous perceptual research, testing in a variety of conditions, provides evidence that subjects do not respond differentially to the calls (Miller *et al.*, 2001; Ghazanfar *et al.*, in prep.; Weiss *et al.*, 2001; Weiss and Hauser, 2002).

Specific Aims

Our goal was to determine whether tamarins call back selectively to an absent cagemate or that antiphonal calling is mediated by a more general absence of individuals from the population. To test between the predictions, we removed from the colony room 2 individuals—A1 and B1—that were living in separate cages, rotating through the colony until each individual had served as A1 5 times and as B1 5 times. We then played back only A1's calls, and recorded the first individual from the colony room to respond. If caller identity mediates antiphonal responding, versus mere physical absence, then when A1's call is played, A1's cagemate—A2, still in the colony room—should respond first. If physical absence mediates antiphonal calling, then both A2 and B2 should respond since both of their cagemates are absent. Based on prior acoustic analyses and playback experiments, we predicted that cues to individual and cage group identity were sufficient to elicit selective antiphonal responding (Weiss *et al.*, 2001; Weiss and Hauser, 2002).

Procedure

We tested 11 adult tamarins over a period of 8 mo, between 1600–1800 h. We conducted 55 trials, consisting of 5 playbacks from each individual. Only one individual's call was played back per trial. The order in which we removed individuals was counterbalanced. Because all individuals are removed for other experiments several times a day during the week, our procedure does not constitute an unusual event for the tamarins.

Before each trial, we removed A1 and B1, living in separate cages from the homeroom and placed them in the playback chamber, acoustically isolated from the homeroom. We then recorded a 1-min baseline period of calling from the homeroom, counting all spontaneous long calls produced in the absence of a playback. As activity patterns of the monkeys vary from day to day, and the events within the homeroom may cause more excitement on one day than on the next day at the same time, we aimed to obtain the most reliable baseline data by recording on the same day at the same time as the experiment. Because experimenters and staff enter the homeroom *ca.* 30–100 times each day, spending variable periods of time in the room, our presence in the colony room during experiments was not unusual.

Following the baseline, we played a CLC from one of the removed subjects via an Alesis Monitor 1 speaker located near the hallway scale. We matched the intensity of the signal (55-75dB) to the range produced by naturally vocalizing tamarins. The distance between the colony room and the scale was 7.2 m. The door of the colony room was kept closed, as is typical during the day. Although the door may slightly distort the acoustics of the call, the setup actually mimicked naturally occurring vocal exchanges.

Inside the homeroom, 2 experimenters recorded audio and visual responses to the playback (Sony Hi 8 Handycam; Sennheiser MKH60P48 directional microphone [50 Hz-20,000 Hz] and Tascam DAT. Outside the homeroom another experimenter played back the stimulus and recorded the session onto the same DAT tape. Due to the arrangement of cages in the homeroom, it was not possible to set up one video camera and simultaneously observe all cages at once. Therefore, we obtained audio and video records from the 2 most likely groups of respondents. Based on a pilot study in which one subject was removed from the colony room and its call played back to the colony, we observed that the subject's cagemate(s) was the most likely respondent on 82% of all trials. Consequently we concentrated focal observations on the 2 cages from which individuals were removed before playbacks. Although the approach does not allow for absolute blind coding of the response we believe that observer biases are unlikely. Further, this more closely approximates field studies of primate communication. The experimenter recording in the room knew the identity of the individuals removed from the colony room, but did not know which of their calls would be used in the playback. Because of the proximity of cages in the colony room, and the length of the long call response (2–3 sec), we were readily able to identify callers from both focal and non-focal cages and subsequently did not need to use our video recordings for the analyses.

Via audio recordings, we measured when all calls were produced using a real-time spectrographic display (Engineering Design, Belmont). Responses consisted of an antiphonal long call produced by a tamarin in the homeroom within 5 sec after presentation of A1's long call. If no tamarin in the homeroom called back to the stimulus within this period, we scored a no-response trial (Ghazanfar *et al.*, 2001; Weiss *et al.*, 2001). The first animal to respond, in all cases, was the first individual to begin its call, which was unambiguous, and onset never co-occurred with other individuals. Although other tamarins sometimes called after the first caller, we did not analyze the data because it was not possible to distinguish between a response to the playback and a response to the first caller.

RESULTS

Tamarins are more likely to respond antiphonally to calls from an absent cagemate than to calls from other absent individuals.

We conducted statistical analyses on 95% of trials, excluding 1 trial in which male RJ responded first and 2 trials in which female SH responded first. Although RJ and SH were, in all 3 cases, the first caller to respond to their removed cagemates, we excluded the data because their baseline call rates before the playback were equal to the call rates after the playback, making it impossible to distinguish between spontaneous and antiphonal calling responses. Of the remaining 9 subjects, only one individual called at all during baseline periods, and its calling rate was half of that recorded post-playback.

For trials in which antiphonal calling occurred, A2 called back first to A1 calls in 21 trials, B2 called back first to A1 calls in 7 trials, and another non-cagemate (C) called back first to an A1 call in 1 trial, which is significantly different than what would be predicted by chance ($\chi^2(2) = 21.79$, $p < 0.001$). In our computation, chance is calculated in a very conservative fashion, assuming random responses should be equally distributed among members of the A, B, and C cages (C cages should actually receive a higher proportion since there are many more cases classified as C than as A or B). In the remaining 23 trials, there was no response (Figure 2; Tables II and III).

In a separate analysis we investigated whether the distribution of responses varied by the sex of the caller. We grouped the subjects by sex and found no dependency on distribution ($\chi^2(3) = 4.21$, $p < 0.24$). In addition, we analyzed whether the distribution of responses differed as a function of cage group, independent of sex. The results revealed that the responses did not differ as a function of cage group when grouped by either the caller's

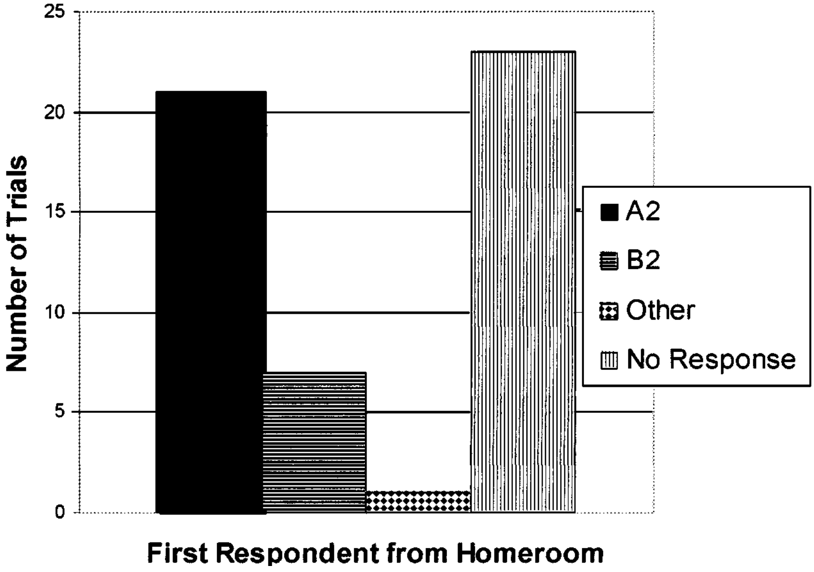

Fig. 2. Results showing the first antiphonal caller from the homeroom within 5 sec. A2 represents the cagemate of the individual that was removed from the homeroom and whose call was played back. B2 represents the cagemate of the other individual that was removed with A2.

Table II. Data for analysis by caller's cage (A-group)

Cage group	Response by A	Response by B	Response by other (C)	No response
1	3	0	0	5
2	3	3	0	4
3	4	2	1	3
4	3	0	0	1
5	4	2	0	4
6	4	0	0	6

Table III. Proportions of responses by caller's cage (A-group)

Cage group	Response by A	Response by B	Response by other (C)	No response
6	0.4	0	0	0.6
3	0.4	0.2	0.1	0.3
2	0.3	0.3	0	0.4
5	0.4	0.2	0	0.4
1	0.38	0	0	0.63
4	0.75	0	0	0.25
Overall average	0.44	0.12	0.02	0.43

(A) cage ($\chi^2(15) = 13.34$, $p < 0.58$) or the B group cage ($\chi^2(15) = 14.45$, $p < 0.49$).

Of the 14 trials in which a response was obtained from A2 and in which A1 had both a mate and offspring in its cagegroup, the mate antiphonally called first during 79% of the trials, while an offspring called first during the remaining 21% of the trials. In 3 of the 4 cages with offspring, the mate antiphonally called first on 100% of the trials.

DISCUSSION

The antiphonal response is mediated by a tamarin's ability to identify certain calls as belonging to a cagemate, versus responding to any long call produced by a physically separated member of the colony. Our results therefore provide further support for the hypothesis that tamarins call back to a visually separated cagemate based on the acoustic signature of the call that provides information about both individual and group identity (Weiss *et al.*, 2001), and not because of mere physical absence.

Our results also add to an understanding of the variables underlying antiphonal calling in cotton-top tamarins. Weiss *et al.* (2001) found that tamarins in an acoustically and visually isolated chamber do not respond preferentially to the long calls of their mates versus those of other colony members. In contrast, our results show that separated cagemates call back selectively to each other in the context of the homeroom. Because offspring did not call back as often to their absent cagemates as did mates, the results provide further evidence that the CLC functions as a contact call between mates, which is similar to that of pygmy marmosets (Snowdon and Cleveland, 1980).

A relevant question, both methodologically and theoretically, is why cotton-top tamarins call back selectively in the context of their homeroom and not in the context of an acoustic isolation chamber (Ghazanfar *et al.*, 2001; Weiss *et al.*, 2001). One possibility, which has yet to be formally tested, is that tamarins consider their homeroom cages as territories, whereas the acoustic isolation chamber represents a neutral space—one lacking in distinctive olfactory markings, nest boxes, and other features. If tamarins represent these spaces differently, then the structure of the receiver's antiphonal calls—and their function—may differ among contexts. This idea is supported by results from a study on common marmosets which show acoustic differences between long calls produced by isolated individuals versus those produced by individuals in a group setting (Norcross and Newman, 1993). Given the evidence for modification during call production based on social context, it is not surprising that we also find vocal responses are affected by changes in social context. Independently of how the issue is resolved, the different patterns of antiphonal responses emphasizes the importance of using different methods to explore similar problems. Had we restricted our analyses to antiphonal calls produced in the acoustic isolation chamber during habituation-discrimination tests, we would have only gained evidence for the tamarins's capacity to discriminate individuals by voice. Our study provides evidence that tamarins actually use these abilities for cagemate, and perhaps individual, recognition.

Another finding from our experiment is that a large proportion of trials elicited no response. It is unknown how frequently this phenomenon occurs in the wild. There may be potential costs, e.g., alerting predators, associated with producing long calls that preclude individuals from responding to every call. If this were true, one might expect call rates to be affected by mating status or kinship. Another possibility is that the response rates are unique to the laboratory setting. Our subjects experience separation regularly, often hearing the CLCs of a mate removed for an experiment multiple times per day from the hallway. Thus the colony may have reached a certain level of habituation to the experience.

Our results indicate that tamarins selectively antiphonally call to an absent cagemate rather than the calling being mediated by a more general absence of individuals from the population. This result is based only on the long calls of known individuals that are absent from the homeroom. Future studies may use calls produced by an unfamiliar individual played to the colony when all group members are present. Given that the CLC may also play a role in mating (Cleveland and Snowdon, 1982, Miller *et al.*, 2001), it would be especially interesting to look for sex differences in antiphonal calling in this situation.

We have argued that our results provide evidence of vocal recognition at the level of either cagemate or individual. However, the robustness of this finding may, be contingent on the specific setup of our tamarin colony. At the time of study, the composition of the colony had been stable for over a year, with no birth or rearrangement of the cage locations or compositions. During this period, analyses by Weiss *et al.* (2001) revealed that in addition to acoustic signatures at the level of individuals and sex, there were also group level signatures. Studies by Jorgensen and French (1998) on Wied's black tufted-ear marmosets indicate that call structure remains stable within a period of *ca.* 1 yr, and then changes. If we assume that cotton-top tamarins undergo similar changes in call morphology, perhaps studies conducted during different periods, associated with changes in colony configuration, will yield different patterns of antiphonal calling. Future work must therefore focus on the plasticity of the combination long call, the capacity for sex and group level signatures, and the roles they play in group cohesion and vocal interactions.

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REFERENCES

Cleveland, J., and Snowdon, C. T. (1982). The complex vocal repertoire of the adult cotton-top tamarin (*Saguinus oedipus oedipus*). *Z. Tierpsychol.* 58: 231–270.

Ghazanfar, A. A., Flombaum, J. I., and Hauser, M. D. (manuscript in preparation). Sex and volubility in cotton-top tamarins: An experimental study of long calling behavior.

Harcourt, A. H., Stewart, K., and Hauser, M. D. (1993). The social use of vocalizations by gorillas: I. Social behaviour and vocal repertoire. Behaviour 124: 89–122.

Jorgensen, D., and French, J. A. (1998). Individuality but not stability in marmoset long calls. Ethology 104: 729–742.

McGregor, P. K., and Dabelsteen, T. (1996). Communication networks. In Kroodsma, D. E., and Miller, E. H. (ed.), *Ecology and Evolution of Acoustic Communication in Birds*, Cornell University Press, Ithaca, NY, pp. 409–425.

Miller, C. T., Miller, J., Gil da Costa, R., and Hauser, M. D. (2001). Selective phonotaxis by cotton-top tamarins. Behaviour 138: 811–826.

Mitani, J. C., and Stuht, J. (1998). The evolution of nonhuman primate loud calls: Acoustic adaptation for long-distance transmission. Primates 39: 171–182.

Norcross, J. L., and Newman, J. D. (1993). Context and gender-specific differences in the acoustic structure of common marmoset (*Callithrix jacchus*) phee calls. *Am. J. Primatol.* 30, 37–54.

Owings, D. H., and Morton, E. S. (1998). *Animal Vocal Communication: A New Approach*, Cambridge University Press, Cambridge, UK.

Rendall, D., Seyfarth, R. M., Cheney, D. L., and Owren, M. J. (1999). The meaning and function of grunt variants in baboons. *Anim. Behav.* 57: 583–592.

Snowdon, C. T., and Cleveland, J. (1980). Individual recognition of contact calls by pygmy marmosets. *Anim. Behav.* 28: 717–727.

Snowdon, C. T., Cleveland, J., and French, J. A. (1983). Responses to context- and individual-specific cues in cotton-top tamarin long calls. *Anim. Behav.* 31: 92–101.

Waser, P. M. (1982). The evolution of male loud calls among mangabeys and baboons. In Snowdon, C. T., Brown, C. H., and Petersen, M. R. (eds.), *Primate Communication*, Cambridge University Press, New York, pp. 117–143.

Weiss, D. J., Garibaldi, B. T., and Hauser, M. D. (2001). The production and perception of long calls in cotton-top tamarins (*Saguinus oedipus*): Acoustic analyses and playback experiments. *J. Comp. Psychol.* 115: 258–271.

Weiss, D. J., and Hauser, M. D. (2002). Perception of harmonics in the combination long call of cotton-top tamarins (*Saguinus oedipus*). *Anim. Behav.* 64(3): 415–426.

West, M., and King, A. (1996). Eco-gen-atics: A systems approach to the ontogeny of avian communication. In Kroodsma, D. E., and Miller, E. H. (eds), *Ecology and Evolution of Acoustic Communication in Birds*, Cornell University Press, Ithaca, NY, pp. 20–38.