

SELECTIVE PHONOTAXIS BY COTTON-TOP TAMARINS (*SAGUINUS OEDIPUS*)

by

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Summary

When nonhuman animals vocalize, signal receivers are provided with a range of potential acoustic information concerning the signaler's body size, sex, individual identity, kinship and group membership. Here we explore whether cotton-top tamarins (*Saguinus oedipus*) extract such information from their species-typical combination long call using a modification of the phonotaxis assay originally designed for studies of anurans and insects. In each trial, we sequentially played long calls produced by two different individuals and then provided test subjects the choice to approach either speaker location. We quantified selective phonotaxis using two different aspects of subjects' behavioural response: the first approach following stimulus presentation and the total number of times subjects approached toward each speaker location. Results from subjects' first approach indicated that tamarins perceived acoustic differences between long calls produced by cagemates, non-cagemate colony members and foreign tamarins. Specifically, males showed a preference to approach foreign females over familiar ones, while females approached cagemate and homeroom males over foreign males. When the total number of approaches made towards each stimulus was analyzed, results revealed that subjects did not selectively approach cagemates over colony members or colony

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members over foreign tamarins. Subjects did, however, approach cagemates significantly more often than foreign tamarins. Overall, these results suggest that (i) tamarins are able to use acoustic information encoded within a single vocal signal to assess individuality and degree of familiarity, and (ii) the phonotaxis assay, successfully used in research on anuran and insects, is also a powerful tool for studies of nonhuman primate communication.

Introduction

Nonhuman animal vocal signals provide a wealth of information to perceivers including information about a caller's affective state (Evans & Marler, 1995), individual identity (Caldwell & Caldwell, 1965; Cheney & Seyfarth, 1980; Tooze *et al.*, 1990; Rendall *et al.*, 1996; Sayigh *et al.*, 1999), group membership (Marler, 1970; Hauser, 1992; Boughman & Wilkinson, 1998; Smolker & Pepper, 1999; Snowdon & Elowson, 1999), dominance rank (Cheney *et al.*, 1995), body size (Ryan, 1980; Fitch, 1997), sex (Weiss *et al.*, in press), fitness (Zahavi, 1975), and the objects or events encountered (Seyfarth *et al.*, 1980a, b; Evans *et al.*, 1994; Hauser, 1998; Zuberbuhler *et al.*, 1999). Because such a rich array of acoustic information is encoded within a vocal signal, perceivers must, at some level, select which component of a signal is most important at any given time with respect to initiating a response. Hence, an individual's behavioural response to a vocalization is context-dependent, contingent upon information that is relevant to a specific social or ecological context (Rendall *et al.*, 1999). Given the range of information encoded within a vocal signal, however, it is often difficult to determine the causal relationship between specific features of the signal and the consequent behavioural response.

The most effective way to address this problem is to employ experimental techniques to assess how animals extract meaningful information from their species-typical vocalizations (*e.g.* Ryan, 1980; Cheney & Seyfarth, 1982; Gerhardt, 1988; May *et al.*, 1988; Nelson & Marler, 1989; McComb *et al.*, 1993; Searcy *et al.*, 1995; Wilczynski *et al.*, 1995; Fitch, 1997; Hauser *et al.*, 1998; Ghazanfar *et al.*, 2001; Miller & Ghazanfar, in press). A series of elegant field playback experiments on vervet monkeys (*Cercopithecus aethiops*) by Cheney & Seyfarth (1988) illustrate the effectiveness of experimental assays in addressing this issue. The first series of experiments used two acoustically distinct intergroup calls, wrrs and chutters, to test whether subjects classified the call based on its acoustic structure or external referent.

Cheney & Seyfarth first habituated subjects to exemplars of one intergroup call type (*e.g.* a wrt). Then following habituation, subjects were tested with an exemplar of the other type of intergroup call (*e.g.* a chatter). Results indicated that if the same caller was used in both the habituation and test phase of the experiment, subjects transferred habituation to the new call type. For test trials in which caller identity changed between habituation and the test, subjects showed an increase in arousal. In a second series of playbacks, Cheney & Seyfarth employed the same procedure, but used two different alarm calls as stimuli. Results indicated that subjects again showed an increased response when caller identity switched between habituation and test trials. In contrast to the intergroup call experiments, however, subjects also showed an increased response on trials in which the caller was constant between the habituation and test, but call type changed. These data suggest that vervets are able to extract information about the callers' identity as well as the calls external referent, thus providing evidence that primates are capable of extracting multiple levels of information from a single vocal signal (*e.g.* Gerhardt, 1992).

Here we employed a phonotaxis assay, initially designed for use in anuran research (Ryan, 1980, 1985; Gerhardt, 1987; Ryan *et al.*, 1990; Ryan & Rand, 1995; Wilczynski *et al.*, 1995; Wilczynski *et al.*, 1999), to explore whether cotton-top tamarins (*Saguinus oedipus*) can extract acoustic information on individuality, group membership and familiarity from their species-specific 'combination long call' (Cleveland & Snowdon, 1981; Weiss *et al.*, in press). The 'combination long call', hereafter CLC, is comprised of a concatenation of temporally distinct syllables (see Fig. 1) and is typically produced while animals are isolated from the group (Cleveland & Snowdon, 1981; Ghazanfar *et al.*, 2001; Weiss *et al.*, in press). As such, they are classified as contact calls.

Acoustic analyses of CLC's produced by one colony of cotton-top tamarins showed consistent structural differences between individuals, sexes and groups housed in the same colony room (Weiss *et al.*, in press). As a result, we can assume that information on these parameters is encoded within the long call. Additionally, since all tamarins in the colony room are in visual and auditory contact with each other, and have been for several years, it is likely that subjects distinguish between familiar (*i.e.* from within the homeroom) and unfamiliar (*i.e.* foreign) tamarins on the basis of their long calls. Furthermore, evidence suggests that tamarins can extract some of

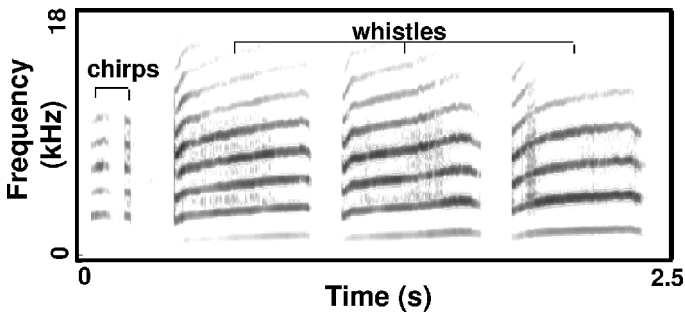


Fig. 1. Spectrogram of a 'Combination Long Call'. The x-axis indicates time, while the y-axis denotes frequency. The two syllable types that comprise the CLC are shown.

the encoded acoustic information in two experimental contexts. In a series of habituation-discrimination playback experiments, Weiss *et al.* (in press) showed that cotton-top tamarins are able to discriminate between CLCs produced by different individuals. Thus, having habituated to CLC exemplars from one individual, subjects dishabituated to a CLC test exemplar from a new individual, but transferred habituation to a new CLC test exemplar from the same individual. Using an antiphonal calling assay (*e.g.* Ghazanfar *et al.*, 2001), Ghazanfar and colleagues (in prep.) showed that tamarins are more likely to antiphonally call when played an exemplar produced by a female than a male tamarin suggesting that members of this species are able to extract information about the caller's sex. Given these observations, we predicted that multiple levels of acoustic information are encoded within CLCs (*i.e.* individuality, group membership and familiarity) and that tamarins are capable, under certain conditions, of extracting this information. The purpose of this study was to (i) build upon earlier work by providing converging evidence that a species of nonhuman primate can extract multiple levels of acoustic information encoded within a single vocal signal, and (ii) successfully employ the phonotaxis assay in a species of nonhuman primate. Specifically, our goal was to assess whether the phonotaxis assay would elicit selective approach behaviour, indicative of perceptual discrimination across multiple acoustic dimensions.

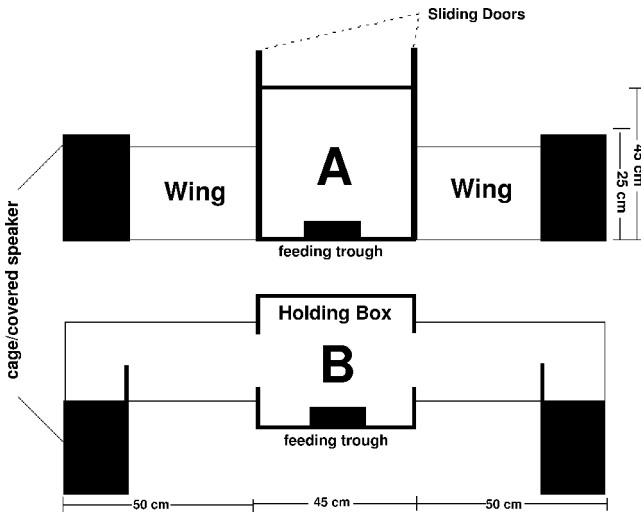


Fig. 2. Schematic drawing of the experimental apparatus. The main sections and features of the apparatus are labeled. (A) shows the front view, (B) shows a view of the apparatus from above.

Methods

Subjects

Ten adult cotton-top tamarins (*Saguinus oedipus*), five females and five males, served as subjects in this experiment. All ten subjects completed each test condition. Subjects were born at the New England Regional Primate Center, Southborough, MA and housed at the Primate Cognitive Neuroscience Laboratory, Harvard University for the duration of the experiment. Their daily diet consists of monkey chow, mealworms, crickets, fruit, peanuts and yogurt; water is provided ad libitum throughout the day. Cages consist of a breeding pair, and in some cases, 1-2 generations of offspring. All subjects previously participated in a range of auditory perception experiments involving both species-typical acoustic signals (Ghazanfar *et al.*, 2001; Miller *et al.*, 2001; Weiss *et al.*, in press) and human speech (Ramus *et al.*, 2000; Hauser *et al.*, 2001). Two additional subjects were initially run in this experiment, but failed to complete any test trials and were dropped from the experiment. The first subject showed excessive frenetic behaviour during the familiarization sessions prior to the first test session and thus was not run on any experimental conditions. The second subject failed to respond to the stimuli during the first test session on two consecutive test days and was not tested further.

Apparatus and equipment

The experimental apparatus consisted of three separate areas, the central holding box, the approach wings and the cages/covered speakers at the ends of each wing (shown in Fig. 2). The entire apparatus was constructed of a wooden frame and wire mesh. The holding box was used to restrict the range of movement of tamarins during the early stages of the experiment. Opening the two sliding doors (Fig. 2) permitted tamarins access to the two adjacent approach

wings. Situated at the end of each wing was either a cage (for familiarization trials) or a covered speaker from which CLCs were broadcast (for test trials). To center subjects during stimulus presentation, and thus avoid potential biases in terms of proximity to one side speaker, we placed a plastic food trough inside the holding box against the front wall.

Experimental conditions

We presented subjects with CLCs produced by individuals in three different stimulus classes: cagemates, familiar non-cagemates and foreign tamarins not residing in the colony. Across all conditions, we presented male subjects with female CLCs and female subjects with male CLCs. Evidence suggests that tamarins may respond differentially to CLCs produced by males and females (Ghazanfar *et al.*, in prep.). By only presenting subjects with CLCs produced by the opposite sex, we controlled against this potential confound. In condition 1, we presented subjects with CLCs produced by their cagemate and a foreign tamarin. In condition 2, we presented subjects with CLCs from their cagemate and a familiar non-cagemate. In condition 3, we presented CLCs produced by a familiar non-cagemate and a foreign tamarin.

Stimuli

All CLCs were recorded prior to testing while subjects were isolated from other tamarins in an acoustic chamber. We recorded CLCs onto a digital audiotape (DAT, Tascam DaP1 Digital Audio Tape Recorder, sampling rate: 48 kHz) using a Sennheiser ME66 directional microphone (frequency response 50-20,000 Hz). All CLCs were then digitally acquired from the digital audiotape onto a Power Macintosh 7100/80 using Sound Designer II acoustics software and an Avid[®] Audiomeia II card. All calls were normalized to peak amplitude. Exemplars of CLCs used as stimuli were free of all background noise and consisted of 1-2 chirps and 3-4 whistles. All CLCs were broadcast to subjects with Advent[®] AV570 speakers at an equal sound pressure level of 8-10 dB above background noise from each speaker using SoundEdit 16.2 acoustics software. As subjects were situated approximately 60 cm from the sound sources, amplitude attenuation was minimal with subjects hearing the signal at approximately 7-9 dB above background noise.

Two exemplars of CLCs were used for each individual (cagemates, familiar non-cagemates and foreign) whose calls were selected for use in the experiment. The stimulus class described as 'cagemates' consisted of CLCs produced by an adult of the opposite sex in their homecage (4 males, 5 females). For nine of the ten subjects, this individual was the subject's mate. The one exception to this rule was an adult female who was still housed with her parents. The CLC stimuli used as the 'cagemate' for this individual were produced by her father. The stimulus class 'familiar non-cagemates' consisted of CLCs produced by individuals (4 males, 4 females) housed in the Primate Cognitive Neuroscience Laboratory homeroom, but not in the same cage as the test subject. In each condition using a 'familiar non-cagemate' CLC, the exemplars used as stimuli were produced by either the adult male or female in the adjacent cage. In most cases, the CLC stimuli used as 'cagemates' for one test subject were also used as 'familiar non-cagemates' stimuli for a different subject. The stimulus class described as 'foreign' tamarins consisted of CLCs produced by individuals (2 males, 2 females) who had previously resided in the colony, but had deceased several years (5-7) before this experiment took place. None of the subjects in this experiment were housed in the Primate Cognitive Neuroscience Laboratory simultaneously with the individuals whose

CLCs were used as 'foreign' tamarin stimuli in the experiment. Since all of the adults in this study were born in the New England Regional Primate Center, it is possible that some individuals had experience with each other while housed at that location. There is no way to determine whether any individuals were housed near each other and for how long. However, given the time elapsed between any previous exposure to each other, the density of animals housed at the NERPC (up to twenty per cage in 15-20 cages per colony room) and the consistency with which all subjects responded to foreign tamarin CLCs (see below), it is reasonable to assume that any previous experience did not effect subjects' response in this experiment.

General procedure

Prior to testing, two Froot Loops[®] were broken into four pieces each and mixed with wood shavings in the food trough inside the testing apparatus (Fig. 2). We removed a subject from its home cage and carried him/her, via transport box, to the testing room. Inside the testing room, we released the subject into the holding box within the experimental apparatus. Subjects participated in six familiarization trials prior to each test session. The familiarization trials prior to the first test session served to habituate subjects to the apparatus. Thereafter, we used familiarization trials to extinguish side biases developed during test sessions. Data on subjects' behaviour were not collected during familiarization trials.

Familiarization session

Familiarization sessions consisted of two trials. In a familiarization trial, we released subjects into the holding box and restricted them to this area for 30 seconds. This duration was approximately the same duration as stimulus presentations during test sessions. After the initial 30 seconds, we raised the sliding doors and permitted subjects to freely move around the entire apparatus for two minutes. Thus an entire familiarization trial lasted for 2 min 30 s. When subjects completed the first trial, we removed them from the apparatus and brought them to a sound proof room in a different part of the laboratory. We then replenished the Froot Loops and ran the second familiarization trial. Once we completed both familiarization trials, we returned the subject to its homeroom cage. Each familiarization session lasted approximately ten minutes. We conducted a single familiarization session per day for a given subject.

Test session

A test session consisted of two different trial types: a familiarization trial and a stimulus presentation trial. The familiarization trial accomplished two things. First, it allowed us to observe subjects' behaviour and assess their general level of arousal prior to testing. We aborted the session prior to testing if subjects exhibited high levels of arousal, indicated by excessive jumping and calling. Second, by having two trials, the procedure used in both the familiarization and test sessions was similar. Upon completion of the familiarization trial, we removed subjects from the apparatus and placed them in a sound proof room in a separate area of the laboratory. During this time, we replaced the wire cages at the end of each wing with covered speakers and replenished the Froot Loops in the food trough.

Five seconds after we released subjects into the holding box, we broadcast a series of four long calls (two exemplars from each of the two individuals) from the covered speakers using

a five second inter-stimulus interval in a semi-randomized order. A single CLC from each of the individuals representative of the stimulus classes for that condition were randomized and presented first, followed by a CLC exemplar from each of the same individuals in a randomized order. For example, subjects might be presented with CLCs in one of the following orders: A1, B1, B2, A1; B1, A1, B2, A2. The entire stimulus presentation period lasted approximately 30 s. Following stimulus presentation, we opened the sliding doors permitting subjects to range throughout the entire apparatus for 60 s. If subjects did not leave the holding box and approach one of the speakers within one minute, we aborted the test session and repeated it on a subsequent day. If a subject did not respond to the test stimuli on two consecutive days, the subject was dropped from the experiment ($N = 1$). We randomized the order of the stimulus presentation for each individual in each experimental condition. Similarly, we counterbalanced the side of the apparatus from which we broadcast each stimulus class between individuals and conditions. Subjects showing no response to the stimuli (*i.e.* not entering either wing following stimulus presentation) were retested on the same stimuli 3-7 days following the initial test. Each test session lasted approximately 10 minutes.

Data collection and analysis

We recorded all trials onto videotape using a JVC Digital Video Camera. Using the 60 s of the test session, an experimenter blind to condition recorded the initial approach following stimulus presentation and the total number of times subjects entered each wing. This 60 s period was somewhat arbitrary, but chosen based on the observation that after 60 s subjects no longer seemed to be responding to the test stimuli. Typically after 60 s, subjects either ran frenetically around the apparatus or remained in the center box and did not approach either speaker location. Subjects were considered to approach the speaker location when at least the front feet and upper half of the body were clearly seen in that wing. In order for subjects to be scored as having multiple approaches, subjects needed to completely re-enter the center holding box before a second approach could be scored. We analyzed each condition individually to determine the patterns of selective phonotaxis for each stimulus pair. Subjects' first approach following stimulus presentation was scored as 1, while the non-approached side was scored as 0. The total number of approaches made toward each speaker location was tallied based on the criteria described above.

As this is the first phonotaxis study in a species of nonhuman primate, it was not possible to assess in advance which aspects of behaviour would be indicative of acoustic discrimination. Subjects first approach response indicates whether an initial acoustic discrimination between the stimulus classes was made, while the number of approaches indicated whether the difference between the stimuli elicited robust differences in the frequency of approach toward either speaker location. This behavioural pattern is considered independent of whether an initial discrimination was made because it shows a bias to approach one stimulus over an extended period of time. In other words, subjects might discriminate between the stimulus classes, but not find the difference sufficient to elicit a significant behavioural bias other than the initial approach.

Based upon findings that female red-bellied tamarins (*Saguinus l. labiatus*) are more responsive to long calls produced by males from their natal population than foreign males (Masataka, 1988), we predicted that if female subjects could perceive differences between the two presented stimulus classes, they would show unidirectional selective phonotaxis towards

the more familiar of the two stimuli. In addition, several studies from our lab show that males and females typically show relatively similar responses to CLCs (Ghazanfar *et al.*, 2001; Weiss *et al.*, in press). Therefore, prior to our experiment, we predicted that both males and females would show similar unidirectional patterns of selective phonotaxis. Based on these predictions, all paired statistical comparisons are one-tailed.

Results

First approach

We tested whether cotton-top tamarins were able to discriminate between long calls produced by individuals from three different stimulus classes (cagemate, familiar non-cagemates, foreign). The one condition in which both males and females behaved similarly was in the cagemate *vs* familiar non-cagemate experiment. In this condition, subjects showed a preferential bias to approach the cagemate over the familiar non-cagemate (Binomial, $p = 0.05$, power = 0.38). In the familiar non-cagemate *vs* foreign tamarin condition, subjects as a group showed no selective phonotaxis towards either of the two stimuli (Binomial, $p = 0.17$, power = 0.15). However, males showed a preferential bias to approach the foreign female over a familiar female from the homeroom, while females consistently approached familiar non-cagemate males over foreign males ($\chi^2_{(1)} = 4.29$, $p = 0.03$, $\phi = 0.7$). Subjects showed no overall selective phonotaxis towards either stimulus class in the cagemate *vs* foreign tamarin condition (Binomial, $p = 0.45$, power = 0.01). In this condition, however, males consistently approached foreign females over their cagemate, while females showed the opposite pattern, approaching cagemates over foreign males ($\chi^2_{(1)} = 3.60$, $p = 0.05$, $\phi = 0.6$). Raw tallies of first approach preferences for all subjects are presented in Table 1.

Number of approaches

To determine whether the number of times each individual entered the two wings of the apparatus indicated a bias towards one of two stimuli across all conditions, we conducted a repeated-measures ANOVA. These data were not transformed as they were normally distributed. We calculated each individual's condition-specific bias by subtracting the number of times an individual approached the more unfamiliar of the two stimuli from the

TABLE 1. *Number of first approaches made by males and females towards each stimulus class for each experimental condition*

Sex of subject	Experimental conditions		
	Cagemate	vs	Familiar non-cagemate
Male:	4		1
Female:	4		1
	Familiar non-cagemate	vs	Foreign
Male:	2		3
Female:	5		0
	Cagemate	vs	Foreign
Male:	1		4
Female:	4		1

number of times the individual approached the more familiar of the two stimuli. Thus, a positive number indicates a preference for the more familiar of the two stimulus classes, while a negative number indicates a bias to approach the more unfamiliar stimulus class more frequently. This analysis revealed no main effect of condition ($F_{2,16} = 1.83$, $p = 0.19$) or sex ($F_{1,8} = 0.46$, $p = 0.5$) suggesting that subjects consistently approached the more familiar of the two stimuli across all conditions irrespective of sex. There was, however, a significant interaction between sex and condition ($F_{2,16} = 18.71$, $p = 0.0001$), indicating that males and females did not show the same preferential pattern across all conditions.

We conducted analyses of each condition individually to determine how the preferential approach patterns within the conditions varied. Although there was some preference for both males and females to approach cagemates (mean = 2.0, SD = 2.1) over familiar non-cagemates (mean = 1.1, SD = 1.2), this pattern did not reach statistical significance (Wilcoxon signed rank: $z = 1.41$, $p = 0.08$). In the familiar non-cagemate vs foreign condition, both sexes showed a preference to approach familiar non-cagemates (mean = 3.2, SD = 2.2) over foreign animals (mean = 1.8, SD = 1.4), but this difference also failed to reach statistical significance (Wilcoxon signed rank: $z = 1.61$, $p = 0.06$). A similar lack of overall selective phonotaxis was observed in the cagemate vs foreign condition (Cagemate: mean = 2.5, SD = 1.9; Foreign: mean = 2.2, SD = 2.1; Wilcoxon signed rank: $z = .29$, $p = 0.38$), but a statistically significant interaction between sex

and approach bias was evident ($F_{1,8} = 22.04$, $p = 0.001$). In this condition, males preferred to approach foreign females, while females preferred to approach cagemates.

Discussion

The experiments reported here were designed to test whether cotton-top tamarins can extract acoustic information about individuality, group membership and familiarity from a species-specific long call in the context of a two-speaker phonotaxis assay. We presented subjects with CLCs produced by their cagemates, familiar non-cagemates and unfamiliar foreign tamarins in all possible paired combinations. We predicted that tamarins would behave in one of four ways. First, subjects might not perceive any differences between the three stimulus classes from the long call alone or not find the differences meaningful within the context of this experimental task. If correct, then subjects should not show consistent approach biases in any condition. Second, subjects may only discriminate between their cagemate and all other tamarins. If correct, then subjects should show a consistent approach pattern in trials that include their cagemate, but approach at random in the familiar non-cagemate *vs* foreign condition. Third, subjects may only be able to distinguish between all familiar and unfamiliar tamarins. In this case, tamarins should not be able to distinguish between their cagemate and familiar non-cagemates and show no selective phonotaxis towards either of the stimulus classes. The tamarins should, however, show consistent approach patterns for all conditions except the cagemate *vs* familiar non-cagemate condition. Fourth, subjects might perceive meaningful differences between all three stimulus classes. If correct, then tamarins should exhibit consistent approach biases across all conditions.

Results from the first approach data indicate that tamarins show selective phonotaxis in each of the three experimental conditions. This suggests that subjects perceived meaningful differences between the three stimulus classes using acoustic information encoded within the CLC, thus supporting the fourth prediction. Given that acoustic information about individuality, group membership and familiarity are encoded within the CLC (Weiss *et al.*, in press), it is possible that this information was extracted by tamarins in this experiment. An alternative explanation, however, is that subjects only used

acoustic information on individuality and familiarity to discriminate between the stimulus classes in each condition. If subjects were able to recognize each individual's CLC in the colony, then all discriminations could be made on the basis of whether the individual was familiar or unfamiliar. If this hypothesis is correct, then acoustic information concerning group membership was not used and our subjects' behaviour was mediated by individuality and familiarity. Our experimental design does not allow us to explicitly test which of these explanations best accounts for the perceptual discriminations made by tamarins. At this time, we have evidence that acoustic differences exist in the CLCs produced by individuals in different cages, but not that this information plays a functional role when discriminating between cagemates, familiar non-cagemates and foreign tamarins. Therefore, the more parsimonious explanation is that tamarins are capable of making discriminations between the three stimulus classes using only individuality and relative familiarity.

Overall, we observed a consistent sex difference in subjects' first approach bias across the experimental conditions. Specifically, it appeared that males were more likely to approach foreign females over both cagemates and females from the homeroom, while females consistently approached the most familiar animal in each condition first, preferring cagemates and familiar non-cagemate males to foreign males. The one condition in which this pattern did not emerge was in the cagemate *vs* familiar non-cagemate condition. Here both males and females showed a preferential bias to approach cagemates over individuals from the homeroom. Although this condition is consistent with the behaviour of females across all conditions, it is inconsistent with the males' behaviour in the other two conditions. This pattern suggests that male tamarins initially approach completely novel females, but when presented with two somewhat familiar females (*e.g.* cagemate and familiar non-cagemate female), approach cagemates first. The exact reason why this pattern emerged is difficult to explain. Although homeroom females are somewhat novel to males, it may be that male tamarins consider homeroom females too familiar to preferentially approach them over cagemates. In other words, the males' strategy may be to approach cagemates, except when presented with a completely unfamiliar female.

In addition to subjects' initial response, we also recorded a second measure as a means of determining whether different aspects of behaviour would provide converging evidence of the first approach or be indicative

of other aspects of auditory perception. Rather than restrict our analyses to subjects' initial approach, we also scored the total number of approaches made to each speaker during the session. Although this measure provided important information suggesting slightly different response patterns, it is also clear that some methodological modifications to the current experimental design are necessary to enhance the robustness of this measure. In the current experimental design, all stimuli were broadcast prior to releasing subjects from the holding chamber. This procedure did not update subjects as to the locations of the stimuli during the experiment. If, however, CLCs were broadcast continuously during the experiment, this information would be provided to subjects and might elicit an increased frequency of approach to one of the two sides. An experiment currently underway employing this modified procedure has successfully elicited more robust behavioural responses from subjects. This improved method will hopefully improve our ability to assess the tamarins' capacity for acoustic discrimination.

Studies of several primate species provide suggestive evidence that individuality (Snowdon & Cleveland, 1980; Cheney & Seyfarth, 1980, 1988; Chapman & Weary, 1990; Cheney *et al.*, 1995; Hammerschmidt & Fischer, 1996; Rendall *et al.*, 1996; Weiss *et al.*, in press) and group membership (Cheney & Seyfarth, 1982; Hauser, 1992; Fischer, 1998; Wilson *et al.*, 2001) are encoded within nonhuman primate vocal signals. To date, however, no single study has attempted to show whether nonhuman primates attend to these different features within a single vocal signal. Here we provide evidence that at least two levels of information, individuality and relative familiarity, can be extracted from a vocal signal using a two-speaker phonotaxis assay, thus supporting the findings of Cheney & Seyfarth (1988). Our results are suggestive that group membership may also be extracted from CLCs, but further testing is required to elucidate this possibility. Additionally, this study shows that, as with studies of anuran communication, the phonotaxis assay is a potentially important tool for studies of primate auditory perception. By employing similar methodologies on different species, we will be in a better position to determine whether similar perceptual mechanisms underlie auditory perception across a range of different taxa.

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