ANIMAL BEHAVIOUR, 2004, **68**, 713–720
doi:10.1016/j.anbehav.2003.10.028

Sensory biases underlie sex differences in tamarin long call structure

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*(Received 25 April 2003; initial acceptance 30 July 2003;
final acceptance 10 October 2003; published online 23 August 2004; MS. number: A9596R)*

Within the vocal repertoires of many species, both males and females produce acoustic variants of the same call type. Despite the relative salience of the acoustic features that correlate with the caller's sex, little is known about the functional significance of this acoustic cue. Specifically, do conspecifics use this information when making behavioural decisions, implying that it is meaningful to signal receivers? And, if so, what selective pressures underlie the salience of the sex differences in call structure? Here we present a series of phonotaxis experiments designed to address these issues in the cottontop tamarin, *Saguinus oedipus*. We focus on the tamarin combination long call (CLC), a species-specific vocalization consisting of one to two chirps followed by three to four whistles, that functions in the context of social isolation and mate attraction. CLCs produced by males had significantly shorter whistles than those produced by females, although there was some overlap in the sex-specific ranges. Sex differences in the acoustic morphology of CLCs elicited consistent selective phonotaxis, suggesting that this acoustic cue is meaningful to signal receivers and that whistle duration is the primary acoustic feature used to determine the sex of the caller. Males preferred female CLCs consisting of the longest whistles, whereas females preferred male CLCs with the shortest whistles, suggesting that sensory biases in tamarins underlie sex differences in CLCs. These preferences persisted even when stimulus calls contained whistle durations that fell outside the natural range.

Many nonhuman animals use systems of vocal communication to mediate behavioural interactions with conspecifics (Hauser 1996; Bradbury & Vehrencamp 1998). Acoustic analyses show that these vocal signals are typically encoded with information about the caller's individual identity (Sayigh et al. 1990; Tooze et al. 1990), sex (Seyfarth et al. 1980; Vicario et al. 2001; Weiss et al. 2001), species (Emlen 1972; Nelson 1988; Gerhardt 1991) and group membership (Marler & Tamura 1964; Boughman & Wilkinson 1998; Fischer 1998). Evidence suggests that these acoustic cues are meaningful to conspecifics because signal receivers use the information encoded in the signal to guide behavioural decisions (Gerhardt 1992; Ryan 1998; Searcy & Nowicki 1999). Despite the relative significance of these acoustic cues for communicating with conspecifics, little is known about what selective forces act on the structure of vocalizations to facilitate the evolution of these cues.

One candidate mechanism that could influence the evolution of acoustic features in vocalizations is selective pressure imposed on the vocalization by conspecific signal receivers. For example, male anurans produce advertisement calls to attract females to mate (Ryan 2001; Gerhardt & Huber 2002). In a classic series of phonotaxis experiments on the Túngara frog, *Physalaemus pustulosus*, females showed a preference to approach male advertisement calls that consisted of both a whine and chuck over those calls that contained only a whine (Ryan 1985; Ryan & Rand 1990). This preference in females imposes directional selection on males to produce advertisement calls with whines and multiple chucks. Similarly, a study of treefrogs (*Hyla versicolor*) showed that females impose directional selection on call duration and call rate in male advertisement calls, while simultaneously exerting a stabilizing force

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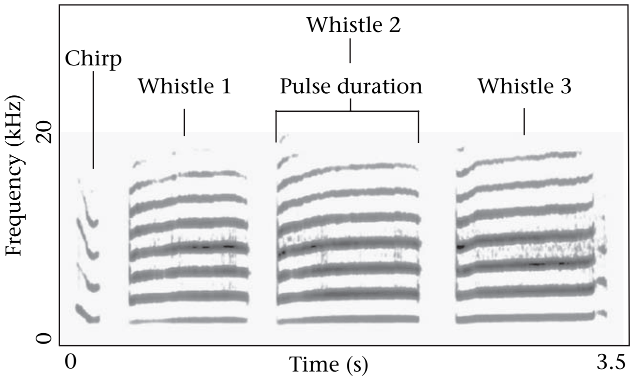


Figure 1. Spectrogram of a cottontop tamarin 'combination long call' showing the two syllable types (chirps, whistles) and pulse duration as measured in the present study.

on the dominant frequency and pulse rate of the call (Gerhardt 1991). For treefrogs, it may be that stabilizing selection facilitates propagating features of the call that enable species recognition, whereas directional selection aids in determining the quality of a mate. Overall, these studies show that preferences in conspecific signal receivers, in the form of sensory biases, can have a significant influence on the structure of species-specific vocal signals. The term sensory bias refers to selective sensitivities in the underlying sensory and/or neural mechanisms that manifest in observable behavioural preferences (Ryan & Keddy-Hector 1992). Such sensory biases have been reported in a range of different taxonomic groups (Ryan 1985, 1998; Christy 1988; Basolo 1990; Searcy 1992; Endler & Basolo 1998; Gerhardt & Huber 2002) and are likely to play an important role in signal evolution.

Given the rich information content of many nonhuman animal vocalizations, sensory biases in signal receivers are likely to influence particular acoustic cues encoded within a vocalization. Here we address this issue in a series of phonotaxis experiments on cottontop tamarins, *Saguinus oedipus*, focusing on the acoustic features used to recognize the sex of the caller. Adult cottontop tamarins produce a species-typical 'combination long call' (CLC) when separated from group members (Miller et al. 2001a; Ghazanfar et al. 2002; Miller & Hauser 2004). The CLC is a multipulsed vocalization consisting of one to two chirps followed by three to four whistles (Cleveland & Snowdon 1982; Miller et al. 2002; Fig. 1), and has been the subject of research both at the level of vocal production (Miller et al. 2003) and perception (for review see Miller et al. 2002). Although both sexes produce this call, acoustic analyses revealed that whistle durations of male CLCs are significantly shorter than those of female CLCs, although some overlap between the sex-specific ranges does occur (Weiss 2000; see Figure 2 in Weiss et al. 2001). In parallel with other primate long calls (Miller & Ghazanfar 2002), CLCs appear to function primarily to mediate group spacing and reestablish contact with group members (Ghazanfar et al. 2002; Miller & Hauser 2004). Recent evidence also suggests that CLCs may function in mate attraction (Miller et al. 2001b).

Here we present a series of phonotaxis experiments that examine the perceptual basis for sex differences in CLCs. We used phonotaxis experiments to address this issue because they allowed us to test both sex discrimination (experiment 1), as well as whether subjects showed a preference for a particular call class within a single sex of callers (experiment 2). Although discrimination and recognition can be assessed using other playback methods (i.e. antiphonal calling, habituation–discrimination), only phonotaxis allows determination of subjects' within-sex preferences in a single experimental trial. Phonotaxis has been used in a range of studies on anurans (Ryan 2001; Gerhardt & Huber 2002) and insects (Gerhardt & Huber 2002), as well as in a recent study of tamarins (Miller et al. 2001b). The primary goal of these experiments was to test whether sensory biases in tamarins underlie the presence and/or salience of the acoustic cues predictive of a caller's sex. However, since this problem can only be explored with prior knowledge of the relevant acoustic features used in recognizing male and female tamarins, we first examined whether tamarins are sensitive to sex differences in CLCs (experiment 1). Building on these results, experiment 2 examined whether tamarins would show selective phonotaxis when presented with CLCs produced by unfamiliar individuals of the opposite sex. We predicted that if sensory biases in receivers underlie sex differences in the acoustic structure of CLCs, male subjects should show selective phonotaxis towards CLCs with the most male-specific features and females should show a bias for CLCs with the most female-specific features.

EXPERIMENT 1

Methods

Subjects

We tested 11 adult cottontop tamarins (five males, six females) in this experiment. All subjects were of breeding age and were the pair-bonded adults from different home cages in our colony. All subjects were born in captivity and socially housed at the Harvard University Primate Cognitive Neuroscience Laboratory. The tamarins' diet consisted of a combination of monkey chow, fruit, sunflower seeds, peanuts and yogurt. Access to water was available ad libitum.

Procedure

Apparatus. We tested subjects in an I-shaped phonotaxis apparatus (Fig. 2a; for a detailed description see Miller et al. 2001b). Selective phonotaxis in this apparatus would indicate that subjects are able to discriminate between two stimuli and that the difference between the stimuli is sufficient to elicit a reliable behavioural response. However, because subjects are positioned between the two speakers, it is not possible to distinguish between a preference to approach one speaker/sound source as opposed to a motivation to avoid the alternative speaker/sound source.

Familiarization trial. Following Miller et al. (2001b), subjects underwent a series of six familiarization trials (three sets of two trials) before testing. These trials served first to familiarize subjects with the test apparatus, and following the initial test, to extinguish any side biases that

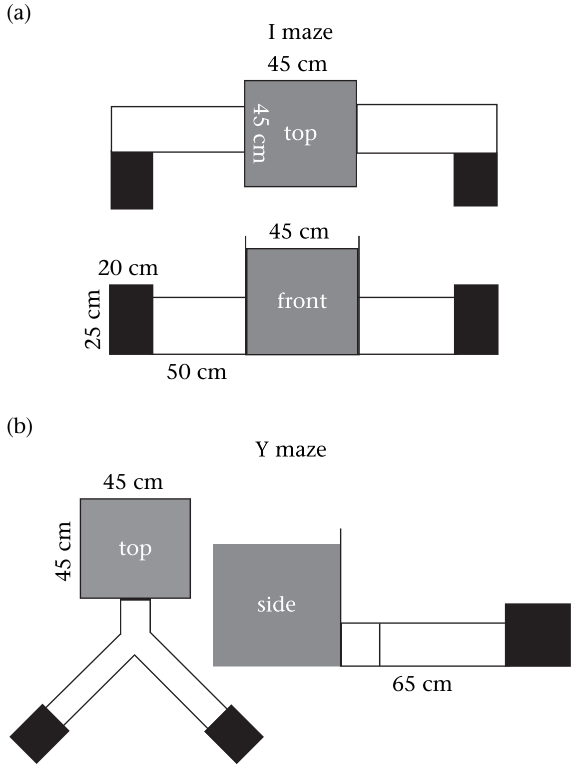


Figure 2. The two phonotaxis apparatuses used: the I maze from experiment 1 (a) and the Y maze from experiment 2 (b).

may have developed due to the previous test. We placed each subject in the centre chamber for 30 s, then raised the doors and permitted the subject full access to the apparatus for 60 s. To provide a spatial and temporal distinction between trials, we removed subjects from the apparatus and carried them via transport cage out of the testing room, then returned them for a second familiarization trial.

Test session. Test sessions consisted of one familiarization trial and two test trials. The procedure for the sole familiarization trial followed the description above. Following the familiarization trial, we removed subjects from the testing room and replaced the transport boxes at the end of each wing of the apparatus with a foam box into which we placed a speaker (Advent Powered Partners frequency range: 70–18 000 Hz; or Alesis Monitor One frequency range: 45–18 000 Hz). To begin a trial, we placed subjects in the centre chamber and broadcast stimuli at a sound pressure level (SPL) of 60–70 dB at 1 m from the speaker to mimic natural vocal output.

We broadcast all stimuli from an Apple G4 computer. Within a test trial, we broadcast six exemplars of CLCs produced by a single individual from one speaker and six exemplars of CLCs produced by one individual from the second speaker. The CLCs used as stimuli in this experiment were produced by tamarins unfamiliar to test subjects (two males, two females). We broadcast stimuli in a manner that simulated a natural vocal interaction. Each trial consisted of six stimulus presentation episodes. An episode consisted of one male and one female CLC broadcast with an interstimulus interval of 5–7 s. We counterbalanced the order of the stimuli between episodes. Episodes occurred at intervals of 10–12 s. During tests, subjects were restricted to the centre chamber of the test apparatus for the first 30 s and exposed to two episodes. Following 30 s, we opened the doors and permitted subjects complete access to the apparatus for 60 s, during which time they received four stimulus episodes. Following the completion of the first test trial, we removed subjects from the test apparatus and placed them in an adjacent room for 3–5 min; we then returned subjects to the test apparatus and began the next test trial.

Test Conditions

Condition 1

We presented subjects with naturally produced CLCs from two unfamiliar males and two unfamiliar females. For each test trial, subjects were presented with one male and one female CLC from each speaker. The whistle durations for the test stimuli and those for the natural range of the population are shown in Fig. 3.

Condition 2

We used the same stimuli as in condition 1, but we manipulated the duration of each whistle in the CLC to be the same between calls using CoolEdit Pro v1.1 (Syntrillium Software 2000). The durations of the whistles in each call were as follows: whistle 1 = 450 ms, whistle 2 = 550 ms, whistle 3 = 500 ms. These durations were chosen because they are within the sex-specific ranges produced by both males and females (Weiss 2000; Weiss et al. 2001; Fig. 3). The interpulse interval was not changed. The identity of the caller differed between test trials and the side and order of stimulus presentation were counterbalanced between subjects.

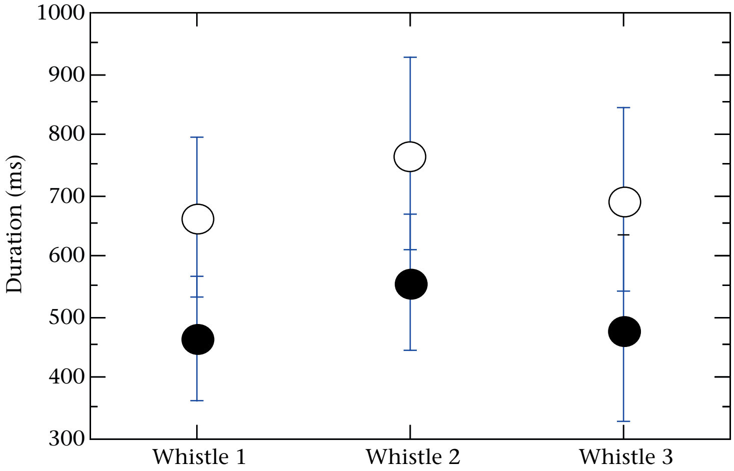
Analysis

All trials were videotaped and coded by two experimenters blind to stimulus type and speaker location. The experimenters coded the wing of the I maze first entered by the subject. We scored an approach if subjects moved at least halfway down one wing of the apparatus (i.e. within 15 cm of the speaker location; ‘first approach’). We eliminated one male from the final data set in condition 2 because he failed to approach either speaker location during two consecutive test sessions. All statistical tests of first approaches were two-tailed with significance set at $P < 0.05$.

Results

Condition 1

Using natural CLCs, subjects approached unfamiliar female CLCs significantly more than unfamiliar male CLCs ($F_{1,10} = 5.38$, $P = 0.04$; Fig. 4). There was no effect of trial ($F_{1,10} = 0.01$, $P = 0.99$) and no interaction between approach and trial ($F_{1,10} = 0.27$, $P = 0.62$), suggesting that subjects’ approach behaviour was consistent across test trials. Analyses revealed no effect of subjects’



	Whistle 1	Whistle 2	Whistle 3
Female population	664.3 ± 130.7	768.6 ± 157.06	693.55 ± 150.3
Female stimulus 1	470.5 ± 105.7	610.2 ± 83.2	516.5 ± 55.6
Female stimulus 2	730.5 ± 140.1	957.1 ± 86.8	774.2 ± 95.3
Male population	464.9 ± 103.9	558.5 ± 111.4	481.5 ± 151.9
Male stimulus 1	555.8 ± 163.8	737.5 ± 88.5	702.3 ± 35.9
Male stimulus 2	288.2 ± 52.7	405 ± 41	463.5 ± 57.9

Figure 3. Sex differences in whistle duration. The graph shows the mean ± SD duration of whistles 1, 2 and 3 for male (●) and female (○) tamarins (data from Weiss 2000; Weiss et al. 2001). Note the overlap in duration between the sexes for each whistle. The table below shows the mean ± SD duration (ms) for male and female populations (data from Weiss 2000; Weiss et al. 2001) and for the calls from two males and two females used as test stimuli in the present experiment. The test stimuli used in the present study were not included in the acoustic analyses performed by Weiss (2000; Weiss et al. 2001).

sex ($F_{1,9} = 0.02$, $P = 0.9$) and no interaction between sex and approach ($F_{1,9} = 0.49$, $P = 0.50$), suggesting that both males and females had the same approach bias across trials.

Condition 2

Using temporally manipulated stimuli, subjects showed no overall preference to approach male or female CLCs ($F_{1,9} = 0.37$, $P = 0.56$; Fig. 4). In addition, there was no effect of test trial ($F_{1,9} = 0.31$, $P = 0.59$) and no interaction between approach and trial ($F_{1,9} = 0.08$, $P = 0.78$), suggesting no difference in approach behaviour across test trials. In addition, there was no main effect of sex ($F_{1,8} = 3.03$, $P = 0.12$) and no interaction between sex and approach ($F_{1,8} = 2.09$, $P = 0.19$), suggesting that both sexes showed similar patterns of approach.

Discussion

In this experiment, we examined whether the acoustic cues known to correlate with the sex of the caller are meaningful to tamarins (i.e. whether information about a caller's sex influences behavioural decisions). Results from experiment 1 allow us to make two points. First, sex differences in CLCs are salient and elicit selective phonotaxis from subjects, suggesting that tamarins are able to recognize the sex of the caller and use this information to make behavioural decisions. Second, a critical acoustic feature used to recognize the caller's sex is whistle duration; this conclusion does not, of course, rule out the possibility that other features are also salient. Although subjects showed selective phonotaxis when presented with CLCs from an unfamiliar male and unfamiliar female tamarin, this effect disappeared when the difference in whistle duration between the sexes was eliminated. Overall, results from experiment 1 suggest that whistle duration is a critical acoustic feature for recognizing the sex of the caller. This finding raises the possibility that sensory biases (Endler & Basolo 1998; Ryan 1998) underlie sex differences in the acoustic morphology of the CLC.

EXPERIMENT 2

The goal of experiment 2 was to test whether tamarins would show selective phonotaxis for CLCs produced by individuals of the opposite sex when whistle duration was systematically varied. Thus, rather than present tamarins with male and female CLCs, we presented subjects with calls produced only by the opposite sex.

Methods

Subjects

Thirteen adult cottontop tamarins (seven males, six females) served as subjects. Twelve of these subjects also participated in experiment 1. All subjects participated in condition 1, and 10 served as subjects in condition 2 (five males, five females). All subjects were of breeding age and were the pair-bonded adults from different home cages in our colony.

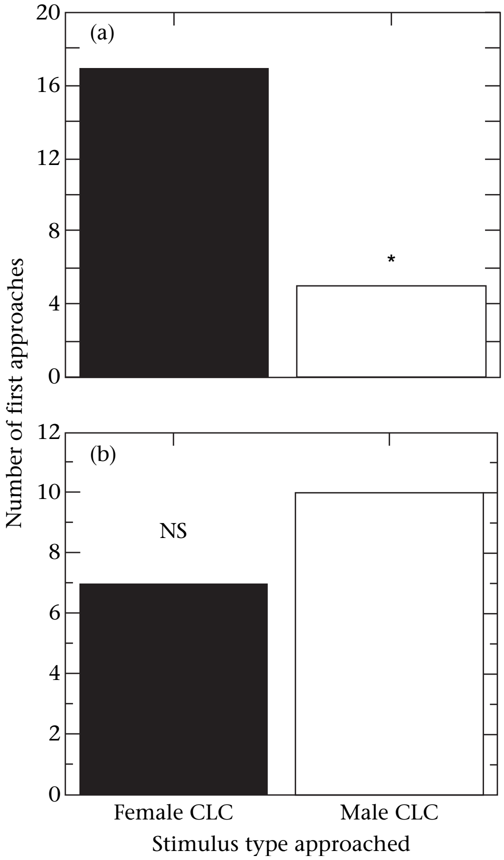


Figure 4. Total number of first approaches that subjects made towards male and female combination long calls (CLCs) in condition 1 (a) and condition 2 (b) of experiment 1. $*P < 0.05$.

Apparatus

For this experiment, we used a Y-shaped test apparatus (Fig. 2b). In contrast to the I maze used in experiment 1, selective phonotaxis in this apparatus provides evidence of both discrimination and a preference to approach one stimulus over another. More specifically, since the furthest distance from each speaker is in the main, starting chamber, an approach to one sound source brings subjects closer to both speakers. This apparatus consisted of a main, starting cage (45 × 45 × 45 cm) similar to that of the I maze, a short base and two branches. A Plexiglas door separated the main cage from the base. A rope connected to the door allowed an experimenter stationed outside of the testing chamber to release subjects into the test apparatus. The base led to two longer branches (25 × 25 × 65 cm) extending 45° away from each other. We constructed the apparatus of wood and used wire for the top, bottom and sides.

Stimulus generation

CLCs produced by the same four unfamiliar animals (two males, two females) used in experiment 1 were also used in experiment 2. We manipulated the pulse durations of the CLCs used as test stimuli for this experiment based on the range in pulse duration reported by Weiss (2000; Weiss et al. 2001; Fig. 3). In condition 1, we generated 'long' and 'short' variants of each CLC based on the sex-specific range in duration. A long variant of the call included whistles with the longest durations in the sex-specific range, while short variants contained whistles with the shortest durations. Whistle durations for long and short variants of female CLCs were: whistle 1 = 950 ms versus 290 ms; whistle 2 = 1100 ms versus 510 ms; whistle 3 = 1100 ms versus 700 ms. Whistle durations for long and short variants of male CLCs were: whistle 1 = 680 ms versus 210 ms; whistle 2 = 760 ms versus 280 ms; whistle 3 = 700 ms versus 220 ms.

For condition 2, we generated a 'within-range' and 'outside-range' version of each stimulus. The within-range stimulus for male and female calls differed in pulse duration. Specifically, female within-range CLCs had pulse durations at the long end of the female range and male within-range CLCs had pulse durations at the short end of the male range. Although the within-female-range CLC stimulus was the same duration as the long variant in condition 1, it was not possible to generate the same manipulation for the within-male-range CLC because whistle duration was already short. Instead, we set the shortest pulse in male CLCs (whistle 1) to be 100 ms and manipulated all durations relative to this whistle. Whistle durations for the within-female-range CLCs were 950 ms, 1100 ms and 1100 ms, and those for the outside-female-range CLCs were 1100 ms, 1290 ms and 1290 ms. Whistle durations for within-male-range CLCs were 260 ms, 260 ms and 280 ms, and those for outside-male-range CLCs were 100 ms, 170 ms and 110 ms. The inter-pulse interval was not changed for the stimuli in either condition.

Procedure

Familiarization. The familiarization procedure was identical to that described for experiment 1.

Test session. The procedure used for test sessions in experiment 2 was identical to that of experiment 1 with two exceptions. First, each test session consisted of one familiarization trial and three test trials, rather than two test trials as in experiment 1. This was done to increase the statistical power of our sample. Because subjects in experiment 1 showed no difference across test trials, we concluded that subjects' selective phonotaxis was likely to be robust enough to continue for an additional test trial. Second, rather than replace the transport box at the end of the branch with a foam box for test trials, we placed a covered speaker at the end of each apparatus wing during the familiarization trials and did not change them during the test trials. We implemented this change because it seemed unlikely that switching the speaker between familiarization trials and test trials had any impact on subjects' behaviour.

Analysis

We coded test trials using the same procedure and statistical tests as in experiment 1.

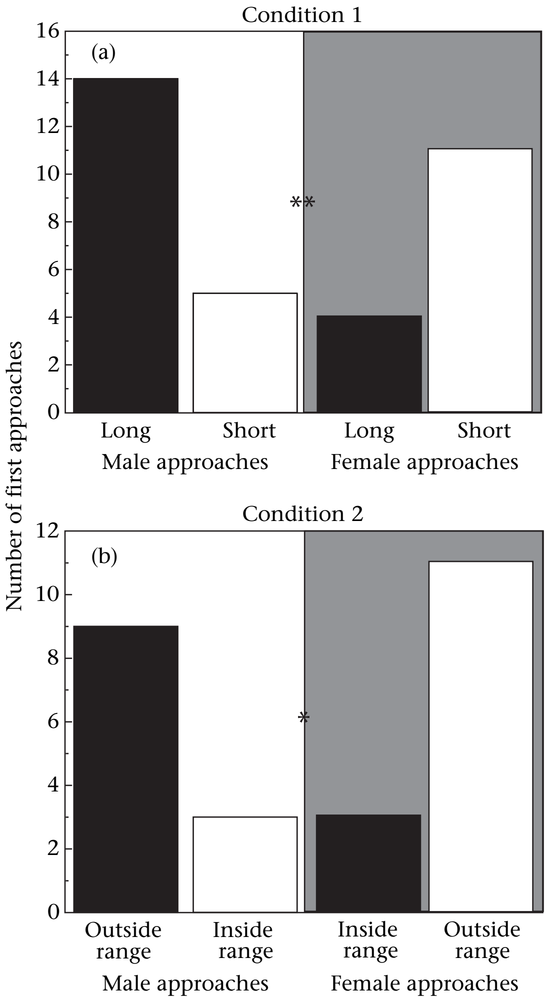


Figure 5. Total number of first approaches that male and female subjects made towards long and short combination long calls (CLCs) in condition 1 (a) and to inside-range and outside-range. CLCs in condition 2 (b) of experiment 2. Note that the male CLC stimuli presented to females in condition 2 were either from the short end of the natural range (inside range) or had whistles that were shorter than those naturally produced (outside range). The female CLC stimuli presented to male subjects in condition 2 were either from the long end of the natural range (inside range) or had whistles that were longer than those naturally produced (outside range). $^*P < 0.05$; $^{**}P < 0.005$.

Results

Condition 1

Analyses revealed that male subjects showed selective phonotaxis towards long female CLCs over short female CLCs, whereas female subjects selectively approached short male CLCs over long male CLCs (Fig. 5). A repeated measures ANOVA testing approach preferences revealed no main effect of approach preference ($F_{1,11} = 0.03$, $P = 0.86$). However, a significant interaction between approach and subject's sex ($F_{1,11} = 13.14$, $P = 0.004$) emerged, suggesting that males preferentially approached long female CLCs and females preferentially approached short male CLCs. There was no three-way interaction between sex, stimulus type and approach ($F_{2,22} = 1.85$, $P = 0.18$), suggesting that the sex differences in approach were consistent across test trials.

Condition 2

Both male and female subjects showed a clear bias to approach test stimuli in which the pulse duration was outside the natural range (Fig. 5). Specifically, males approached the outside-female-range CLC (i.e. longer pulses), and females approached the outside-male-range CLC (i.e. shorter pulses). A repeated measures ANOVA revealed no main effect of approach ($F_{1,8} = 0.20$, $P = 0.67$). As in the previous condition, however, there was a significant interaction between test approach and subject's sex ($F_{1,8} = 9.8$, $P = 0.01$), suggesting that male and female subjects showed selective phonotaxis biases for stimuli with different pulse durations. Specifically, males approached CLCs with longer pulses, and females approached CLCs with shorter whistles. A three-way interaction between subject's sex, approach and test trial was not statistically significant ($F_{2,16} = 3.3$, $P = 0.06$). This nearly significant interaction resulted because, on the first trial, all but one subject approached their respective outside-range stimulus, whereas on subsequent trials, the strength of the bias diminished.

GENERAL DISCUSSION

Many nonhuman animals produce vocalizations encoded with acoustic information about the caller's identity, sex, species and group membership (Gerhardt 1992). However, little is known about the role of different selective pressures on the evolution of these acoustic cues. Here we presented a series of experiments designed to test whether sex-specific perceptual mechanisms, in the form of sensory biases, exert selective pressure on sex differences in the morphology of the tamarin's combination long call. Acoustic analyses indicated that males produce CLCs consisting of shorter whistle syllables than females. As a result, tamarins could potentially use this feature to recognize the sex of the caller. Results from experiment 1 confirmed this hypothesis. Given the significance of this acoustic feature for sex recognition, we next tested whether tamarins have a bias for this feature that might facilitate the sex difference in CLC structure. In experiment 2, females showed selective phonotaxis for male CLCs with the shortest whistle syllables, whereas males preferred female CLCs containing the longest whistle syllables. This pattern of results suggests that tamarins show a selective bias for CLCs consisting of whistle durations that most clearly indicate the caller's sex. Because subjects' preferences persisted even when the whistle durations were outside the naturally produced range, these data suggest that sensory biases in tamarins exert a directional selection pressure on this acoustic feature of CLCs.

To distinguish between these possibilities, we presented subjects with CLCs consisting of pulses at the end of the natural sex-specific range that was preferred in condition 1 and a CLC with pulses outside the natural range in condition 2. Results indicated that the preference shown by subjects in condition 1 persisted in condition 2. Namely, males showed selective phonotaxis for female CLCs with whistle pulses longer than the naturally produced range, and females showed selective phonotaxis for male CLCs with whistle pulses that were shorter than the naturally produced range. These results suggest that tamarins possess sensory biases for whistle durations in opposite-sex CLCs. Subjects' preferences persisted outside the naturally produced range, suggesting that the sensory biases exert a directional selection pressure on this feature of the call.

There are two possible ways to explain the presence of the tamarin's sensory bias. First, the sex-specific sensory biases for pulse duration in CLCs could have existed prior to selection acting on it. This pattern would mirror studies of other taxonomic groups (Basolo 1990; Ryan 1990; Ryan et al. 1990). Alternatively, male and female tamarins may have produced acoustically distinct CLCs prior to any selection on the call and later evolved a sensory bias to select for calls that are least similar to the calls produced by individuals of the same sex, thereby reducing the likelihood of a recognition error (Hurd et al. 1995; Enquist & Arak 1998). The available data are insufficient to determine which of these processes underlies the sensory biases in tamarins. As a result, continued research is necessary to distinguish between these alternatives.

Data from this study, as well as previous studies of tamarins (Miller et al. 2001b) and other primates (Mitani 1985; Wich & Nunn 2002), suggest that long calls may be involved in aspects of primate mating behaviour. However, the role of CLCs in mate attraction differs from anuran advertisement calls in at least two important ways. First, in contrast with anurans, where only the males produce the signal of interest, the tamarin's CLC is produced by both sexes. Second, as opposed to male anuran calls that appear to provide females with all the information necessary to choose a mate, the tamarin's CLC is most likely to be only one of many factors ultimately used by individuals to make decisions about mating. For tamarins, CLCs with clearly perceivable sex differences could be used for mate attraction in the following contexts. Long calls may serve as an initial attractor for individuals searching for an individual with which to form a pair bond. Because males and females emigrate from their social group at least once during their lives (Goldizen & Terborgh 1989), it would be important for both male and female CLCs to contain acoustic features that facilitated attracting a potential mate. Furthermore, despite forming long-term pair bonds, tamarins are known to engage in high rates of extrapair copulations (Sussman & Garber 1987; Dixson 1993). Since tamarins often produce long calls at territorial boundaries, these behavioural encounters provide individuals with acoustic information about the individuals in neighbouring groups. If the acoustic morphology of the CLC contains information that is relevant to the caller's fitness, it might mediate extrapair interactions.

The majority of studies in which sensory biases have been reported have focused on vocalizations or displays that are highly specialized for mate choice (Ryan 1985, 1998; Christy 1988; Basolo 1990; Endler & Basolo 1998; Searcy 1992; Gerhardt & Huber 2002). This pattern suggests that although sensory biases evolve for reasons other than mating, they ultimately play a critical and perhaps exclusive role in mate choice. Our results suggest that sensory biases underlie sex differences in tamarin CLCs. As discussed above, however, this vocalization serves no single function and is used in a range of different contexts. Therefore, it may be that sensory biases can affect vocal signals that have evolved for reasons other than, or in addition to, mate choice (Miller et al. 2001b). However, if the ability to easily recognize the caller's sex is a quality that facilitates mate attraction, then our results are consistent with the notion that sensory biases can only influence vocalizations, or components of calls, that are involved in mate attraction. Given the diverse range of functions that CLCs serve in tamarins, it is unlikely that sexual selection is the only selective force acting on CLCs. Rather, it is more likely that both natural and sexual selection pressures underlie the presence and significance of various acoustic features in CLCs.

Acknowledgments

We thank the many excellent undergraduates who helped run these experiments. Roberto Delgado, Asif Ghazanfar, Brian Hare, Jeff Stevens and two anonymous referees provided excellent comments on the manuscript. Funding for these experiments was provided by a National Institutes of Health NRSA predoctoral fellowship (F31 MH63501) to C.T.M., the Mind, Brain and Behavior Program and the Harvard College Research Program at Harvard University to J.C.S., and by the National Science Foundation (Research on Learning and Education, ROLE) and McDonnell Foundation to M.D.H.

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