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Individual recognition during bouts of antiphonal calling in common marmosets

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Abstract Many vocalizations are encoded with a diversity of acoustic information about the signal producer. Amongst this information content are social categories related to the identity of the caller that are important for determining if and how a signal receiver may interact with that individual. Here, we employed a novel playback method in common marmosets (*Callithrix jacchus*) to test individual recognition during bouts of antiphonal calling. These experiments utilized custom, interactive playback software that effectively engaged subjects in antiphonal calling using vocalizations produced by a single individual and presented 'probe' vocalization stimuli representing a different individual at specific points within bouts of calling. The aim here was to test whether marmosets would recognize that the probe stimulus was a phee call produced by a different individual. Data indicated that marmosets were able to detect the change in caller identity; subjects produced significantly fewer antiphonal call responses to probe than control stimuli and, in some conditions, exhibited a shorter latency to produce the vocal response. These data suggest that marmosets recognize the identity of the individual during bouts of antiphonal calling. Furthermore, these results provide a methodological foundation for implementing the probe playback procedure to examine a broader range of social categorization during vocal interactions.

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Introduction

Vocal communication is commonly influenced by the social relationships of conspecifics (Bradbury and Vehrencamp 1998; Seyfarth and Cheney 2010). The dynamics of behavioral interactions are mitigated by the respective dominance rank, age, sex, familial relatedness and numerous other social characteristics of group members (Bergman et al. 2003; Cheney and Seyfarth 2007). As each of these social categories are encoded in the acoustic structure of vocalizations, species evolved perceptual mechanisms that extract this meaningful information from the signals (Miller and Cohen 2010). Generally, experiments that test recognition during vocal communication examine whether this information can be identified from individual vocalization exemplars, often broadcast as temporally distinct stimuli during playback experiments. Yet many species engage in reciprocal vocal exchanges commonly referred to as bouts. The role recognition plays in mitigating the successive vocalizations occurring during these interactions is not well characterized. Experimentally testing this issue, however, presents certain logistical challenges, as traditional playback methods may not be adequate for testing this dimension of vocal behavior. To this end, we developed interactive playback software that both engages common marmosets (*Callithrix jacchus*) in their species-typical antiphonal calling behavior and allows experimental manipulation of a stimulus class within the bout in order to test aspects of vocal signal recognition and social categorization.

The ability to recognize the individual identity of a caller based on the acoustic properties of a vocalization is widespread among vertebrates (Beer 1970; Waser 1977; Cheney and Seyfarth 1980, 1988; Snowdon and Cleveland 1980; Myrberg and Riggio 1985; Sayigh et al. 1999; Insley 2000; Bee and Gerhardt 2001b, 2002; Aubin and Jouventin 2002; Bergman et al. 2003). Perhaps the most compelling example of individual recognition is in king penguins (*Aptenodytes patagonicus*). Despite interference from thousands of similar voices and a high level of background noise, parents and their nestlings recognize each other's voices and use these cues to reunite when separated (Aubin and Jouventin 1998, 2002; Jouventin et al. 1999). The fact that this form of social categorization is prevalent amongst vertebrate species is not surprising. Species living in stable social groups have repeated interactions with the different conspecifics in their group. Likewise, more solitary species may benefit from recognizing particular individuals. In each circumstance, recognizing the identity of a particular caller would be imperative to making decisions about if, how and when to interact with particular individuals. Presumably such decisions would not be limited to the onset of a vocal interaction, but persist throughout the successive reciprocal exchanges.

Playback experiments are a cornerstone of nonhuman animal vocal communication research. Traditionally, these experiments involve broadcasting a vocalization exemplar and measuring different dimensions of subjects' motor responses (Seyfarth et al. 1980; Nelson 1988; Zuberbuhler et al. 1997, 1999; Nowicki et al. 2001). This assay has proven most useful for elucidating a particular class of phasic vocalizations, acoustic signals, such as alarm calls and various mating calls that communicate a specific message to conspecific signal receivers. These vocalizations, however, represent only a small number of the diversity of vocal signals produced by nonhuman animals (Marler 2004; Miller and Bee 2012). Many vocalizations are commonly produced not only as phasic signals, but in bouts of vocalizations (Schwartz et al. 2002; Sloan and Hare 2004; Miller and Wang 2006; Miller and Bee 2012). Chorusing, for example, is common amongst anurans (Schwartz et al. 2001; Gerhardt and Huber 2002), as is counter-singing in territorial birds (Langemann et al. 2000; Burt et al. 2001; Peake et al. 2005). Traditional playback experiments are inadequate for experimentally probing these vocal behaviors and, as such, interactive playback experiments have been developed to bridge this methodological gap (Dabelsteen and Pedersen 1990; Dabelsteen 1992; McGregor et al. 1992; Schwartz 2001). These interactive designs provide a unique view into not only the communicative content of a signal, but the suite of other meaningful information available to signal receivers based on the context in which the signal is produced. While interactive playback experiments were pioneered in studies of anurans and songbirds, they have recently been implemented in studies of nonhuman primates as well (Miller and Wang 2006; Miller et al. 2009a). Rather than be largely observers in animal communication systems, interactive playback methods allow researchers to actively participate and experimentally probe multiple dimensions of dynamic vocal exchanges, thus elucidating many of the more veiled facets of communication.

Common marmosets are highly voluble New World primates endemic to the forests of Northeastern Brazil (Bezera and Souto 2008; Rylands et al. 2009). This species engages in a vocal behavior known as antiphonal calling that involves the reciprocal exchange of phee calls, a long-distance contact call, between visually occluded conspecifics (Miller and Wang 2006). Previous work employed the first interactive playback experiments in a nonhuman primate species to test the functional significance of call latency for maintaining these vocal interactions (Miller et al. 2009a). This temporal component of the vocal behavior, however, is not the only feature that modulates antiphonal calling in marmosets. The social categories encoded within call structure, such as the caller's individual identity, sex and cage dialect (Norcross and Newman 1993; Miller et al. 2010b), also affect the dynamics of antiphonal calling (Miller and Wang 2006). The aim of this study was to experimentally test whether social categorization for individual identity persists during bouts of antiphonal calling by implementing a new interactive playback design.

Building on our earlier interactive playback technique in common marmosets (Miller et al. 2009a), here we developed software that more directly enabled tests of vocal signal recognition and categorization during vocal exchanges. Similarly to the initial design, here the software is designed to interact with and elicit vocal responses from marmosets during natural, reciprocal antiphonal calling exchanges. The key difference between the two interactive techniques was that the version employed in the present study was designed to present different exemplars of probe stimuli during bouts of antiphonal calling that differed from the baseline set of vocalization stimuli along a testable feature dimension. After a predetermined succession of consecutive antiphonal calls in a bout, a probe (or control) stimulus was broadcast. The 'control' stimulus was simply a different vocalization exemplar from the same category as all other vocalization stimuli used in the experiment (i.e. baseline stimuli). The 'probe' stimulus, however, was an exemplar of a vocalization representing a different category from the baseline stimuli (Fig. 1b). If subjects perceived the probe stimulus as being a distinct category relative to baseline, one would expect subjects to exhibit measurable differences in behavior. If no difference were perceived between the two classes of stimuli, no difference in behavior would be expected.

The rationale of these experiments is somewhat similar to previous playback studies designed to test whether subjects' expectations about a vocalization stimulus were violated based on the preceding stimuli (Nelson 1988; Nelson and Marler 1989; Cheney et al. 1995; Ramus et al. 2000; Bee and Gerhardt 2001a, b; Bergman et al. 2003). Collectively these studies, as well as the present experiment, sought to establish an expectation of a particular stimulus class for the signal receiver and then test whether a new stimulus was perceived as being consistent or inconsistent with the initial stimulus class. In other words, if presented with a series of vocalization exemplars from individual A, vocalization exemplars from individual B would then be presented to determine whether subjects recognized the change in caller identity. There are at least two dimensions, however, that distinguish the probe playback method from these other techniques. First, in contrast to habituation-discrimination experiments (Nelson and Marler 1989; Bee and Gerhardt 2001a, b), our aim was not to habituate the listener. In fact, it is clear that despite continued involvement in antiphonal calling playback experiments, general habituation to the antiphonal calling behavior or playback stimuli does not occur. Second, rather than test subjects' responses as a third party observer to vocal interactions (Cheney et al. 1995; Bergman et al. 2003; Peake et al. 2005), subjects in these experiments were actively involved in the communicative exchange. Eavesdropping and active communication reflect different dimensions of the broader communication networks that characterize how species exchange information with conspecifics (McGregor and Dabelsteen 1996; Miller and Bee 2012). As such, more work is needed to determine the extent to which similar mechanisms for vocal signal recognition and categorization are implemented in each of these contexts.

In this study, we employed the probe playback paradigm in the two following experiments testing individual recognition during antiphonal calling. The first experiment sought to test whether the probe playback technique would be effective at eliciting behavioral responses to changes in social categories. Here, we presented subjects with a probe stimulus—a phee call exemplar from an unfamiliar animal—that would likely be perceptually salient. Experiment 2 built on this result and tested whether subjects were able to recognize individual identity while controlling for familiarity and the sex of the caller serving as the baseline and probe stimulus. The aim of this study was twofold. We sought to both test individual recognition in common marmoset antiphonal calling and establish the probe playback procedure as a technique for further study of vocal signal recognition and categorization at both the behavioral and neural levels.

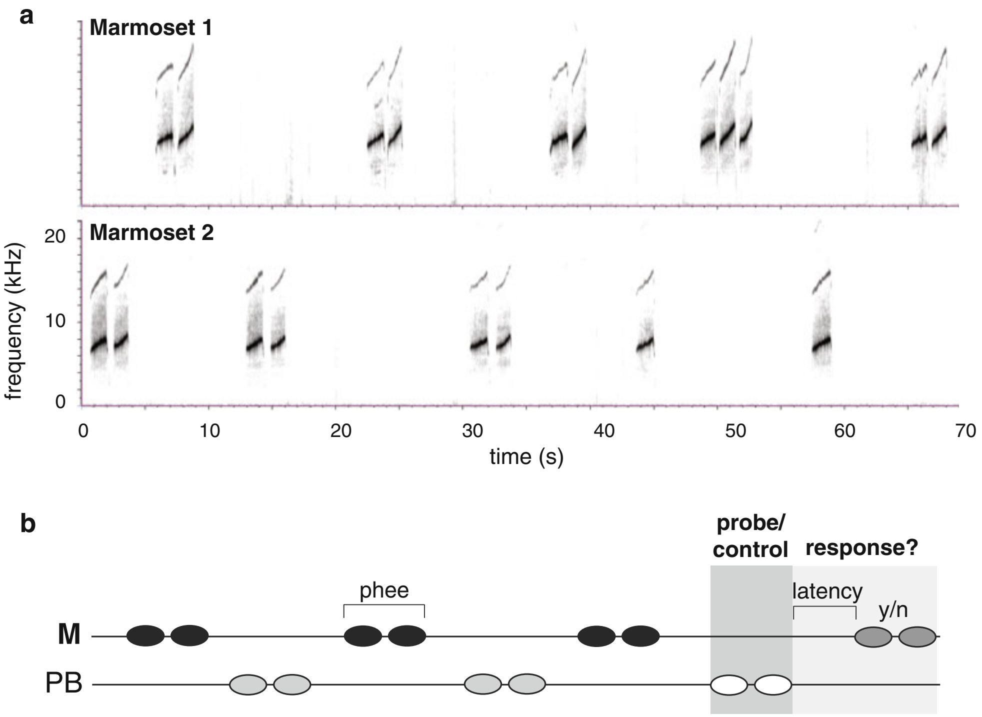

Fig. 1 **a** Spectrogram showing an antiphonal calling bout. *Marmoset 1* is shown above, while *Marmoset 2* is shown below. The vocalizations depicted in the spectrogram are common marmoset phee calls. **b** Schematic drawing of the probe playback procedure. *M* represents the phee calls produced by the subject marmoset. *PB* represents the phee call stimuli presented by the software. The 'probe/control' stimulus is represented as a *white colored* phee call. That time period is shaded in *dark grey*. The response period is shaded in *light grey*. We measured both whether subjects produced an antiphonal call response (*y/n*) and, if a response did occur, the latency to call production

Materials and methods

Subjects

Five adult common marmosets served as subjects in this study: three males and two females. All subjects are socially housed in groups consisting of pair-bonded mates and up to two generations of offspring. The current colony comprises 10 adult marmosets housed as stable pair-bonded male/females in separate cages within the same colony room. As such, all individuals can hear the vocalizations produced by the other animals in the colony and have lived in the colony together for over a year. Only five adult subjects in the colony are sufficiently vocal to be used in playback experiments. This small-bodied New World primate has been the subject of numerous studies investigating the neurobiology and behavior of vocal communication (Norcross and Newman 1993, 1997; Norcross et al. 1994; Wang and Kadia 2001; Eliades and Wang 2003, 2005, 2008b; Miller and Wang 2006, 2011; Pistorio et al. 2006; Bezera and Souto 2008; Miller et al. 2009a, b, 2010a, b; Simoes et al. 2010; Roy et al. 2012).

Experiment procedure

We transported subjects from the colony to the testing room in transport cages. The testing room was 4 m × 3 m in size. The chamber itself is a radio frequency shielded room (ETS-Lindgren) constructed inside a sound attenuated room. The walls and floor of the room are covered in material that absorbs a range of frequencies, including vocalizations. This test chamber is used both for behavioral experiments, such as the one described here, as well as for freely moving and wireless neurophysiology experiments in marmosets (Eliades and Wang 2008a; Miller and Wang 2011). Once inside the room, we placed subjects in a wire mesh test cage. We positioned a free-field speaker (Polk Audio TSi100, Frequency Range: 40–22,000 Hz) 4 m in front of the test cage with a dark curtain equidistant between the subject and the speaker (i.e. both the cage and speaker were 2 m each from the curtain). We broadcast stimuli from a computer through a Crown amplifier (Model D-75A) and the free-field speaker at ~90 dB SPL measured at 1 m from the speaker. In each test session, we broadcast 50 total stimuli. If subjects' volubility for any session was too low, the trial was repeated. Only sessions in which at least six probe and control stimuli were presented are included in this study.

Probe playback procedure

Previously we implemented interactive playback software that effectively engaged common marmosets in antiphonal calling (Miller et al. 2009a). Building on this work, here we developed custom playback software that likewise interacts with subjects during antiphonal calling, but was also capable of presenting probe stimuli as specific events in these vocal interactions. The logic of the design was to first engage subjects in a bout of antiphonal calling. If these interactions reached the bout length threshold (i.e. a predetermined number of consecutive antiphonal calls), an exemplar of the probe/control stimulus class was presented to subjects. Whether subjects produced an antiphonal call response following the probe/control stimulus and, if a response was emitted, the latency to that vocalization was recorded (Fig. 1).

Three classes of phee calls were used in these experiments: baseline, probe and control. Baseline stimuli were a battery of phee calls representing one stimulus class. In the case of the experiments performed here, they were different phee call exemplars produced by a particular individual. A control stimulus was a new exemplar from the baseline stimuli, while the probe stimulus class consisted of phee calls representing a different stimulus class (i.e. a different individual caller here). Typically, each session comprised 8–10 exemplars of the probe and control stimulus classes. Subjects were presented with a different exemplar on each occasion that the respective stimulus class was broadcast. By presenting subjects with different exemplars of these stimulus classes, we controlled for any behavioral effect that was specific to a particular vocalization exemplar.

Similarly to previous work, this software would broadcast a phee stimulus each occasion subjects emitted a phee call (Miller et al. 2009a). For this experiment, these stimuli were presented within 2–3 s of subjects' phee calls. We defined an antiphonal call response as each occasion that subjects produced a phee call within 10 s of a playback stimulus (Miller and Wang 2006; Miller et al. 2009a). A bout was defined as subjects producing an antiphonal call response to consecutive playback stimuli. In other words, following a playback stimulus presentation and subsequent antiphonal call response from a subject, a playback stimulus was presented again and the same sequence of events was repeated. The bout length was measured as the number of successive antiphonal calls produced by subjects.

Probe and control stimuli were each broadcast 50% of the time bout length threshold was reached. Whether a probe or control stimulus was broadcast was randomized across the test session. Different subjects naturally produce bouts of different durations and, therefore, the threshold for each animal was determined by their individual volubility. All subjects were initially tested using a probe threshold of two consecutive phee calls. In other words, the probe/control stimulus was the third playback stimulus in a particular bout. If bouts did not persist for at least this number of calls, a probe/control stimulus was not broadcast. Two subjects were sufficiently voluble to employ a bout length threshold of two calls throughout the experiment. For three subjects, however, insufficient bouts reached this threshold during the first three test sessions. For these subjects, the bout length threshold was reduced to one (i.e. the probe/control stimulus was broadcast as the second playback stimulus in a bout). We did not observe any difference in the general pattern of responses between subjects with different bout length thresholds. A baseline of at least six probe and six control stimuli needed to be presented for the session to be included in the dataset. If subjects failed to reach this level, the session was repeated. Once a bout length threshold was established for each subject, no session was repeated more than once.

Playback stimuli

All vocalization stimuli employed in these experiments were 2-pulsed phee calls. Phee calls used as ‘familiar’ stimuli were recorded during natural antiphonal calling interactions between conspecifics in our colony in the same test chamber used in this experiment. Phee calls used as ‘unfamiliar’ probe stimuli were recorded during antiphonal call exchanges in a similar sound attenuated chamber at Johns Hopkins University (Miller et al. 2010b). In both cases, two subjects were placed in test cages 4 m apart with a cloth occluder placed equidistant between the cages. Sennheiser directional microphones (model ME-66) were positioned 1 m in front of each subject and all vocalizations recorded direct to disk. Two-pulsed phees were extracted from these exchanges and stored according to the individual identity of the caller, as well as whether the call was produced as an antiphonal call response or as a spontaneous call. More details of this procedure can be found in previous studies (Miller and Wang 2006; Miller et al. 2010b) .

Experiments

This study comprised two experiments. Each experiment tested whether subjects would detect a change in caller identity following presentation of probe stimuli during bouts of antiphonal calling. Subjects were run on each condition twice using different stimuli. The order of the conditions was counterbalanced across subjects.

Unfamiliar probe

This experiment consisted of two conditions. In both, the baseline stimuli presented to subjects were phee calls produced by an individual in the UCSD colony. The conditions differed, however, in the probe stimuli presented to subjects.

- *Condition 1: between sex* Here the probe stimuli were phee calls produced by an unfamiliar animal of the opposite sex of the baseline stimuli. This condition was considered to be the most robust in terms of available cues for individual recognition because the change in identity covaried with a change in sex and familiarity. The aim of this condition was to test whether the general playback method could be utilized to study social categorization.
- *Condition 2: within sex* Probe stimuli in this condition were phee calls produced by an unfamiliar animal of the same sex as the baseline stimuli. The aim of this condition was to test whether subjects would detect a change in the caller’s individual identity while controlling for the sex of the caller.

Familiar probe

This experiment also consisted of two test conditions. Both conditions controlled for sex and familiarity as cues for individual identity by only utilizing phee calls produced by animals within the UCSD colony as stimuli. This experiment tested whether marmosets could recognize the identity of the caller and whether any difference in the sex of the caller affected individual recognition.

- *Condition 1: male stimuli* All stimuli used in this test condition were phee calls produced by males. The probe stimuli were calls produced by a different male from the baseline and control stimulus groups.
- *Condition 2: female stimuli* All stimuli used in this test condition were phee calls produced by females. The probe stimuli were calls produced by a different female from the baseline and control stimulus groups.

Data analysis

Analyses focused on subjects’ responses following presentations of probe and control stimuli. Specifically, we compared two aspects of subjects’ behavioral response: antiphonal calls produced and the latency of the antiphonal call response. For each of these behavioral measures, we performed repeated measures ANOVAs comparing responses between control and probe stimuli. An alpha level of $p < 0.05$ (two-tailed) was used for all tests.

Results

Unfamiliar probe

Subjects produced significantly more antiphonal calls in response to control stimuli than to probe stimuli suggesting that subjects recognized the change in individual identity during probe stimulus presentations [$F(1,4) = 19.82$, $p = 0.011$; Fig. 2a]. There was no interaction between the two conditions and stimulus types, suggesting that this general pattern was consistent. While the latency to the antiphonal call response was longer to probe stimuli than controls, this difference was not statistically significant (Fig. 2b).

Analyses of the individual conditions revealed a similar pattern of data (Fig. 2c). In ‘Condition 1: within sex’, all subjects produced more antiphonal calls to control stimuli than probe stimuli. A repeated-measure ANOVA showed this effect to be statistically significant [$F(1,4) = 13.52$, $p = 0.021$]. For ‘Condition 2: between sex’, the same pattern was evident. Significantly more antiphonal calls were produced following control stimuli than probes [$F(1,4) = 20.19$, $p = 0.011$]. Here all but one subject showed the general effect of producing more antiphonal calls in response to control than probe stimuli. No interaction between the effect for condition and session number was evident, suggesting that the pattern of responses was consistent across both test sessions. Furthermore, we observed no significant difference in the latency to respond between the probe and control trials.

Familiar probe

The general trend here followed the previous experiment. Overall, subjects produced significantly fewer antiphonal calls following a probe stimulus than a control stimulus suggesting that the change in the identity of the caller was perceptually salient [$F(1,4) = 27.59$, $p = 006$; Fig. 3a]. A significant interaction did not occur between the two conditions and stimulus types suggesting that this general pattern was consistent. Analyses of response latency revealed an interesting pattern of results. Overall, statistical comparisons of probe and control trials revealed that subjects exhibited a shorter response latency to probe stimuli than control stimuli. This difference was nearly statistically significant [$F(1,4) = 6.25$, $p = 0.065$]. Moreover, a significant interaction was evident between the condition and stimulus type [$F(1,4) = 6.59$, $p = 0.061$]. This suggests that the pattern of responses may vary between the test conditions.

Statistical analysis of the individual conditions revealed a broadly similar pattern of data. In both of the test conditions, all subjects produced more antiphonal calls in response to control than probe stimuli in both of the test conditions. In ‘Condition 1: male stimuli’, subjects were significantly more likely to produce an antiphonal call following a control than probe stimulus [$F(1,4) = 16.64$, $p = 0.015$]. Results from ‘Condition 2: female stimuli’ revealed the same pattern [$F(1,4) = 9.85$, $p = 0.035$]. No interaction was evident between the condition and session number suggesting the same pattern of vocal behavior was evident across the sessions.

In contrast to the previous experiment, subjects did show a significant difference in antiphonal response latency for Condition 1 [$F(1,4) = 15.11$, $p = 0.01$]. Subjects exhibited a shorter latency to produce an antiphonal call in response to a probe than control stimulus. However, no significant difference was evident for this behavioral response in Condition 2. This pattern of results explains the

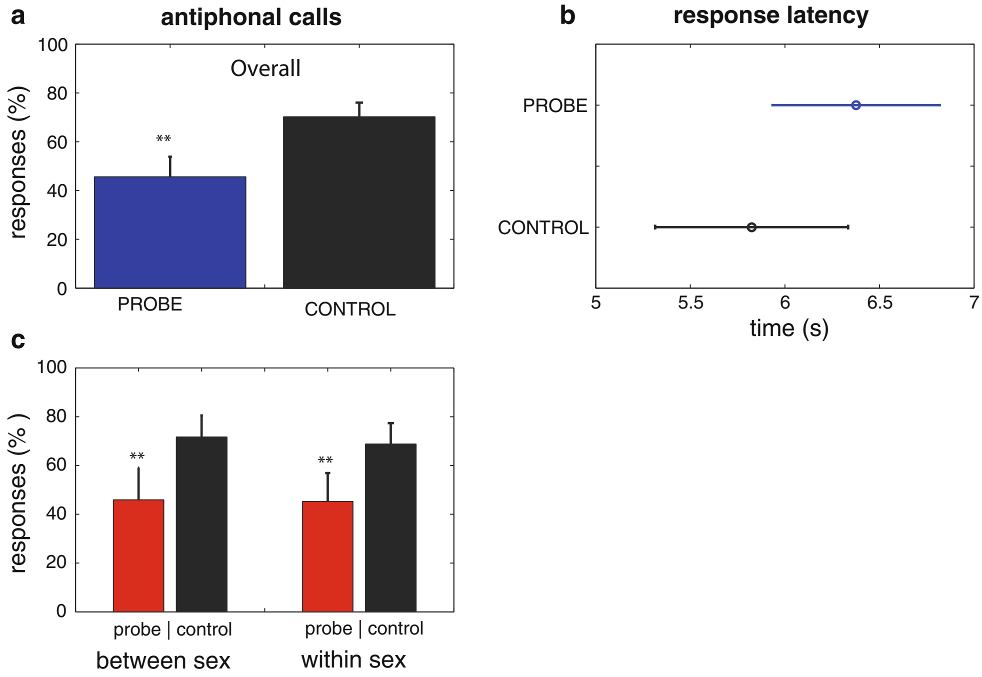

Fig. 2 Results from ‘Unfamiliar’ probe experiment. **a** Bar graph plots the mean (SE) percent of antiphonal calls produced in response to probe (*blue*) and control (*black*) stimuli for both test conditions combined. **b** Plots the mean (SE) latency to respond in seconds for probe (*blue*) and control (*black*) stimuli for both test conditions combined. **c** Bar graphs plot the mean (SE) percent of antiphonal calls produced in response to probe (*red*) and control (*black*) stimuli in each of the individual test conditions: ‘Between-sex’ is shown on the *left* and ‘Within-sex’ is shown on the *right*. *Double asterisks* indicates statistical significance

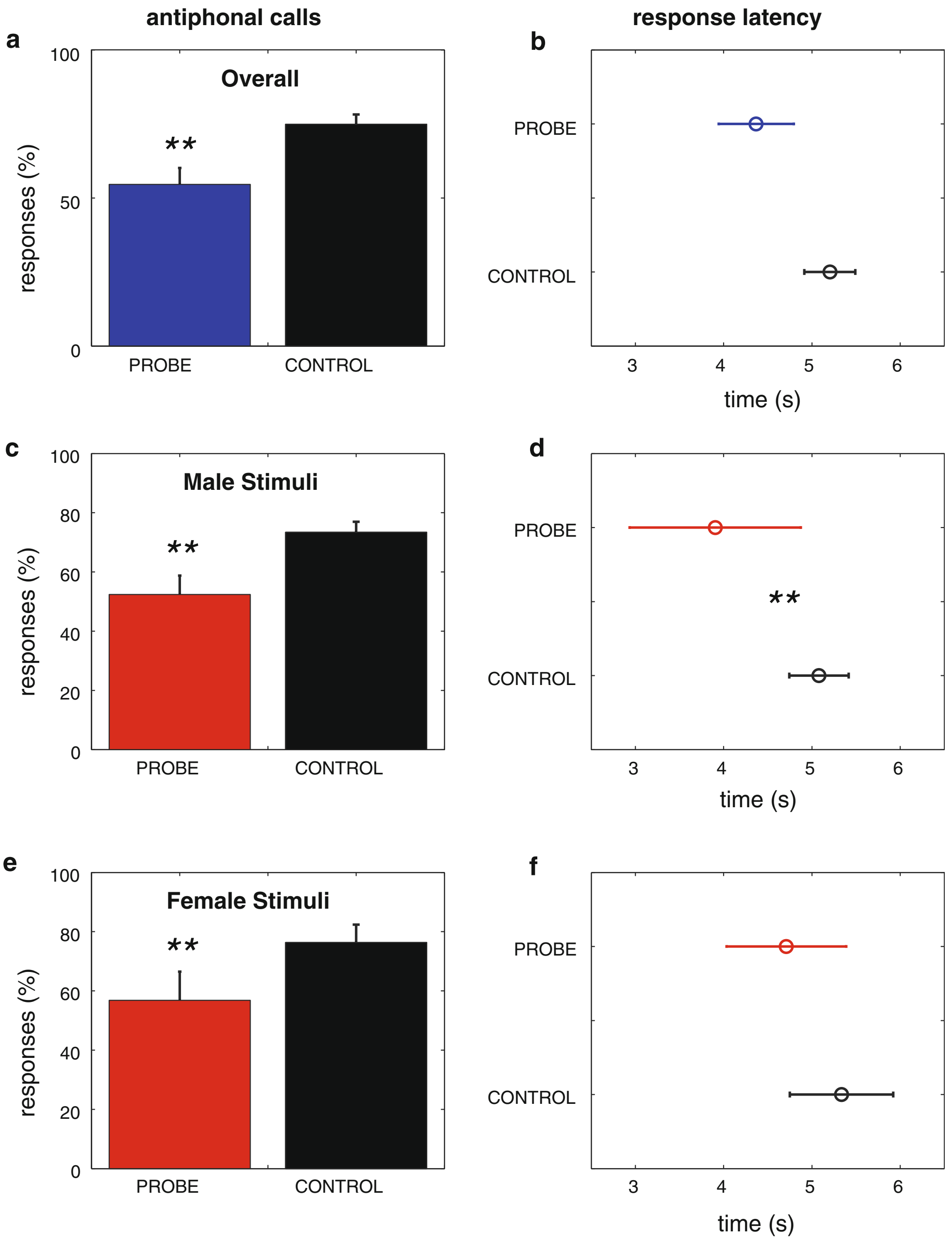

Fig. 3 Results from ‘Familiar’ probe experiment. The *column on the left* plots the mean (SE) antiphonal call responses in bar graphs. The column to the right plots the mean (SE) antiphonal response latency in error bars. (**a**, **b**) Plots the overall data. Probe stimulus data are shown in *blue*, while control data are shown in black. **c**, **d** Plots data for Condition 1: Male Stimuli. Probe stimulus data are shown in *red* and control data in *black*. **e**, **f** Plots data for Condition 2: Female Stimuli. Probe stimulus data are shown in *red* and control data in *black*. *Double asterisks* indicates statistical significance

interaction between test condition and stimulus type in the initial overall analysis above.

Discussion

This study had two primary aims, one methodological and one conceptual. Methodologically, we sought to test whether the probe playback method employed here could be implemented in studies of social categorization. We previously employed interactive playback experiments to test the functional significance of response latency during antiphonal calling (Miller et al. 2009a). Despite evidence that social categories modulated aspects of antiphonal calling (Miller and Wang 2006), our preliminary tests showed that our earlier interactive method was ineffective at eliciting robust changes in the antiphonal calling behavior. The probe playback method was designed to address these earlier methodological shortcomings. More conceptually, we were interested in testing whether marmosets continued to attend to the individual identity of the caller once a bout of antiphonal calling was initiated. The majority of studies tested subjects' social recognition and categorization test subjects' response to temporally isolated vocalization exemplars. Given that many species engage in bouts of vocal exchanges (Farabaugh 1982; Mitani and Gros-Louis 1998; Janik 2000; Gerhardt and Huber 2002), a pertinent question is whether once a bout is initiated the signal receiver continues to parse the social categories (i.e. individual identity) of the signal producer for each successive vocalization produced, or whether that information becomes less pertinent once it is determined by the initiating vocalization. If the former were true, one would expect that experimental manipulation of a social category would be detected at any point in the bout. No behavioral response would be evident if the latter were true.

Data presented here suggest that common marmosets recognize the identity of a caller and that this social category is continually parsed during antiphonal calling exchanges. In the first experiment, we sought to test the validity of the probe playback design by presenting subjects with test stimuli that were particularly salient. Specifically, the probe stimuli were phee calls produced by unfamiliar animals. In both conditions, subjects showed a strong behavioral difference in response to the probe and control stimuli, producing significantly fewer to the former (Fig. 2). Since the phee calls used as probe stimuli were produced by unfamiliar animals, it is possible that subjects' behavioral responses were more simply related to categorizing the callers based on familiarity. In other words, subjects could have simply recognized the one caller as familiar and the probe stimulus caller as unfamiliar without needing to recognize the individual identity of either. The second experiment addressed this issue by controlling for familiarity. Here, both the baseline and probe stimuli used in both conditions were phee calls produced by marmosets from UCSD. As in the first experiment, here subjects showed significant differences in the likelihood of producing an antiphonal call in response to probe and control stimuli. This finding both strengthens the validity of the probe playback procedure and indicates that marmosets categorize callers along at least one social dimension—individual identity—for each consecutive vocalization that occurs in bouts.

The ability to categorize conspecifics along multiple social dimensions from a caller's vocalization appears nearly ubiquitous in vertebrate species (Gerhardt 1992; Miller and Ghazanfar 2002). Amongst highly gregarious species in stable social groups, such as nonhuman primates, this capacity likely occurs effortlessly as individuals navigate the complexities of their social landscape (Bergman et al. 2003; Cheney and Seyfarth 2007). Studies of both wild and laboratory nonhuman primate populations, for example, report an abundance of evidence that signal receivers are able to categorize vocal signal producers according to their respective individual identity (Cheney and Seyfarth 1990, 2007; Miller et al. 2004; Rendall et al. 2004; Miller and Cohen 2010). In fact, a series of studies involving a captive population of cotton-top tamarins (*Saguinus oedipus*) found that conspecifics recognize the individual identity of the caller from the species-typical combination long call using three different methods (Weiss et al. 2001; Miller et al. 2001, 2005). Social categorization, however, is not restricted to individual identity, as information about the caller's sex, rank, dialect, etc. may also be encoded in the acoustic structure of a vocalization and is perceptually salient to conspecifics (Cheney et al. 1995; Bergman et al. 2003; Miller et al. 2004). While the data presented here contribute to a relatively large literature on individual recognition, this methodology can be applied to a broader range of social categories. Acoustic analyses indicate that the marmoset phee call is encoded with other social categories, such as the caller's sex and group membership (Miller et al. 2010b). Future work will implement the probe playback procedure to test the perceptual salience of these categories as well.

The method developed for this study extends our previous work as part of an ongoing research program aimed at developing software that permits the experimental manipulation and quantification of the ongoing dynamics of vocal interactions. As discussed earlier, the experimental design employed here shares some similarities with the more traditional habituation-discrimination technique utilized in previous experimental work in animal communication (Nelson 1988; Nelson and Marler 1989; Cheney et al. 1995; Ramus et al. 2000; Bee and Gerhardt 2001a, b; Bergman et al. 2003). Both techniques involve presenting subjects with exemplars of vocalizations from one stimulus category followed by the broadcast of vocalization exemplars representing a potentially second category. Despite these methodological similarities, data from this study suggests that these experimental designs are equivalent. During habituation-discrimination experiments, subjects typically show a significantly stronger response to 'probe' stimuli than control. Here, we observed the opposite effect; subjects produced fewer antiphonal calls in response to probes than controls. This suggests that subjects are not habituating to vocalization exemplars from a particular category during these experiments, despite hearing multiple exemplars during a session and over the course of a bout. Rather, subjects' responses here suggest that the change in behavioral response is more likely the result of the probe stimulus trials defying its expectation of the identity of the other animal engaged in the interaction.

A long-standing model of animal communication systems is the producer–receiver dyad (Dawkins and Krebs 1978; Guilford and Dawkins 1991, 1993). Within this model, communication is viewed as an isolated event involving one animal producing a signal and a second animal receiving that signal. Conceptually, traditional playback experiments are particularly well suited for this type of signaling system because the signal can be experimentally broadcast and the response of the receiver measured. It has, however, become increasingly evident that these dyads are not representative of all aspects of communication (Miller and Bee 2012). More recently, the notion of communication networks was introduced as a complimentary model to address the wider scope in which signals are exchanged between conspecifics (McGregor and Dabelsteen 1996; McGregor and Peake 2000). These networks often involve multiple callers engaging in more complex, tonic streams of vocal exchanges. In order to experimentally parse this more dynamic social aspect of communication systems, interactive playback experiments will be necessary. As vocal signal recognition and social categorization are likely to play pivotal roles in these networks, procedures like the one employed here will be necessary to test their respective contributions.

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